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A New Genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an Analysis of Its Phylogenetic Relationships

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ABSTRACT

The muroid fossils from Lagoa Santa, Brazil, that Winge described as *Hesperomys molitor* in 1887 are indistinguishable from Recent Uruguayan specimens described by Herskovitz as *Holochilus magnus* in 1955. We synonymize these nominal taxa and diagnose *Lundomys*, new genus, with *molitor* as its type and only valid species. We summarize the morphological characters of Recent and fossil specimens of *Lundomys molitor* and provide comparisons with species of *Holochilus*.

The phylogenetic relationships of *Lundomys* and *Holochilus* (sensu stricto) are analyzed to test the rival hypotheses that *Holochilus* (sensu lato) is more closely related to *Sigmodon* than to *Oryzomys*, or vice versa. Also of interest is the phylogenetic significance of numerous derived similarities among *Holochilus*, *Lundomys*, and *Pseudoryzomys*. The uniquely most-parsimonious tree determined by 25 morphological characters of *Holochilus*, *Lundomys*, *Oryzomys*, *Pseudoryzomys*, and *Sigmodon* suggests that *Holochilus* and *Sigmodon* form a monophyletic group with *Pseudoryzomys* and *Lundomys* as successively more distant sister taxa: ((((*Holochilus*, *Sigmodon*) *Pseudoryzomys*) *Lundomys*) *Oryzomys*). Previous studies of male genitalia and G-banded chromosomes, however, have

suggested that *Holochilus* and *Oryzomys* are more closely related to each other than either is to *Sigmodon*. Because most of the derived similarities between *Holochilus* and *Sigmodon* are dental traits, and because both genera are herbivorous, adaptive convergence is a plausible ad hoc explanation of our phylogenetic results. We hypothesize that other derived traits from functionally diverse anatomical systems are synapomorphies of a monophyletic group that includes *Holochilus*, *Lundomys*, *Pseudoryzomys*, *Zygodontomys*, and oryzomyines (sensu stricto). We diagnose the tribe Oryzomyini accordingly and emphasize differences with previous tribal concepts based on symplesiomorphy.

Natural history information from Recent populations suggests that *Lundomys molitor* is semi-aquatic and occurs in sympatry with *Holochilus brasiliensis* in pampas habitats at temperate latitudes in Uruguay and southernmost Brazil (Rio Grande do Sul). The Lagoa Santa fossils (from the tropical Brazilian state of Minas Gerais) therefore document a considerable range extension northward in the late Pleistocene, probably coincident with global climatic cooling. The paleoecological significance of other Lagoa Santa fossils have been similarly interpreted by previous investigators.

RESUMEN

Los muroideos fósiles de Lagoa Santa, Brazil, que Winge describió como *Hesperomys molitor* en 1887 son indistinguibles de los especímenes Recientes del Uruguay descritos por Herskovitz como *Holochilus magnus* en 1955. Reconocemos estos taxa nominales como sinónimos y describimos *Lundomys*, género nuevo, con *molitor* como su especie típica y única. Resumimos los caracteres morfológicos de los especímenes Recientes y fósiles de *Lundomys molitor* y proporcionamos comparaciones con las especies de *Holochilus*.

Las relaciones filogenéticas de *Lundomys* y *Holochilus* (sensu stricto) son analizadas para probar las hipótesis rivales de que *Holochilus* (sensu lato) está filogenéticamente más cerca de *Sigmodon* que de *Oryzomys*, o viceversa. También es de interés el significado filogenético de numerosos caracteres derivados similares entre *Holochilus*, *Lundomys*, y *Pseudoryzomys*. El árbol más parsimonioso determinado por 25 caracteres morfológicos de *Holochilus*, *Lundomys*, *Oryzomys*, *Pseudoryzomys*, y *Sigmodon* sugiere que *Holochilus* y *Sigmodon* forman un grupo monofilético, con *Pseudoryzomys* y *Lundomys* como taxa hermanos sucesivamente

más alejados: ((((*Holochilus*, *Sigmodon*) *Pseudoryzomys*) *Lundomys*) *Oryzomys*). No obstante, estudios anteriores de la morfología peneal y de bandeo G cromosómico han sugerido que *Holochilus* y *Oryzomys* están filogenéticamente más cerca que cualquier otro lo está de *Sigmodon*. Puesto que la mayoría de los caracteres derivados similares entre *Holochilus* y *Sigmodon* son dentarios, y puesto que ambos géneros son herbívoros, la convergencia adaptativa es una explicación plausible de nuestros resultados filogenéticos. Proponemos la hipótesis de que otros caracteres derivados de sistemas anatómicos funcionalmente diversos son sinapomorfias de un grupo monofilético que incluye *Holochilus*, *Lundomys*, *Pseudoryzomys*, *Zygodontomys*, y oryzominos (sensu stricto). De acuerdo con esto, damos una diagnosis de la tribu Oryzomyini y resaltamos las diferencias entre nuestra clasificación y otras basadas en simplesiomorfias.

La información ecológica sobre poblaciones Recientes sugiere que *Lundomys molitor* es semiacuática y vive en simpatria con *Holochilus brasiliensis* en los hábitats subtropicales y templados

del Uruguay y del extremo sur de Brasil (Rio Grande do Sul). Los especímenes fósiles de Lagoa Santa (desde el estado brasileño tropical de Minas Gerais) documentan, pues, una mayor extensión geográfica hacia el norte en el Pleistoceno tardío, pro-

bablemente coincidiendo con una de las épocas de enfriamiento climático global. El significado paleoecológico de otros fósiles de Lagoa Santa ha sido interpretado de manera semejante por investigadores anteriores.

RESUMO

Os muróideos fósseis de Lagoa Santa, Brasil, descritos por Winge em 1887 como *Hesperomys molitor*, são indistinguíveis dos espécimes Recentes procedentes do Uruguai, que foram descritos por Hershkovitz em 1955 como *Holochilus magnus*. Consideramos ambos os táxons nominais como sinônimos e propomos um novo gênero, *Lundomys*, tendo como única espécie válida a espécie tipo, *molitor*. Apresentamos um resumo das características morfológicas de espécimes Recentes e fósseis de *Lundomys molitor* e o comparamos com espécies de *Holochilus*.

As relações filogenéticas de *Lundomys* e *Holochilus* (sensu stricto) são analisadas a fim de testar duas hipóteses concorrentes, que consideram *Holochilus* (sensu lato) mais aparentado com *Sigmodon* do que com *Oryzomys*, e vice versa. Também é de interesse o significado filogenético de numerosas semelhanças derivadas entre *Holochilus*, *Lundomys*, e *Pseudoryzomys*. A partir da análise de 25 características morfológicas de *Holochilus*, *Lundomys*, *Oryzomys*, *Pseudoryzomys*, e *Sigmodon*, a árvore filogenética mais parsimoniosa sugere que *Holochilus* e *Sigmodon* formam um grupo monofilético, tendo como grupos irmãos sucessivamente mais distantes *Pseudoryzomys* e *Lundomys*: ((((*Holochilus*, *Sigmodon*) *Pseudoryzomys*) *Lundomys*) *Oryzomys*). No entanto, estudos anteriores baseados na genitália masculina e nos cromossomos preparados para bandas "G" sugeriram que *Holochilus* e *Oryzomys* seriam mais

proximamente aparentados entre si do que cada um é com *Sigmodon*. Uma vez que a maior parte das semelhanças derivadas entre *Holochilus* e *Sigmodon* é baseada em características dentárias, e devido ao fato de que ambos os gêneros são herbívoros, a convergência adaptativa é uma explicação ad hoc plausível de nossos resultados filogenéticos. Estabelecemos a hipótese de que outras características derivadas de diferentes sistemas funcionais anatômicos constituem sinapomorfias de um grupo monofilético que inclui *Holochilus*, *Lundomys*, *Pseudoryzomys*, *Zygodontomys*, e orizomiíneos (sensu stricto). Assim, propomos uma nova diagnose da tribo Oryzomyini e enfatizamos as diferenças de conceitos tribais anteriores baseados em simplisimorfias.

Informações sobre a história natural de populações Recentes sugerem que *Lundomys molitor* é uma forma semi-aquática e ocorre simpatricamente com *Holochilus brasiliensis* nos habitats de pampas em latitudes temperadas no Uruguai e na parte sul do Brasil (Rio Grande do Sul). Desta maneira, os fósseis de Lagoa Santa (procedentes do estado tropical brasileiro de Minas Gerais) documentam uma considerável ampliação da distribuição para o norte durante o Pleistoceno tardio, possivelmente coincidente com o resfriamento climático global. O significado paleoecológico de outros fósseis de Lagoa Santa foram interpretados de maneira similar por outros pesquisadores.

INTRODUCTION

Among the many specimens of fossil mammals excavated by Peter Wilhelm Lund from caves near Lagoa Santa in central Brazil (Voss and Myers, 1991) are several cranial fragments of a large rat that Winge (1887) named *Hesperomys molitor*. Apparently unknown from living specimens, *molitor* was listed as an extinct Pleistocene form of *Oryzomys* by Trouessart (1898) and the name subsequently vanished from the literature of Recent mammalogy for over half a century. The species

is not included in the synopses of Neotropical muroids prepared by Gyldenstolpe (1932) and Tate (1932), nor does it appear in Moojen's (1952) treatise on Brazilian rodents or Cabrera's (1961) monumental catalog of South American mammals. Hershkovitz (1962) listed *molitor* as a Pleistocene species of *Calomys*, but no other 20th-century mention of the name preceded Massoia's (1980) suggestion that *molitor* closely resembles *Holochilus magnus*, a Recent but apparently uncom-

mon semiaquatic species from Uruguay and southern Brazil.

Colin Campbell Sanborn collected the type series of *Holochilus magnus* in Uruguay in 1926 but did not recognize that his specimens included two sympatric kinds of marsh-dwelling rats; in a summary report (Sanborn, 1929), all were identified as *H. vulpinus*. Sanborn's mistake was eventually discovered by Hershkovitz (1955) who described *H. magnus* and illustrated many of its diagnostic characters. For Hershkovitz (1955, 1962, 1966), the genus *Holochilus* belonged to a small assemblage of herbivorous muroids, the "sigmodont" group (also including *Neotomys*, *Reithrodon*, and *Sigmodon*), distinguished from other Neotropical genera by their distinctively flat-crowned, lophodont molars.

To test Massoia's (1980) hypothesis, we borrowed the type material of *Hesperomys molitor* from the Universitets Zoologisk Museum in Copenhagen and compared it with all of the specimens of *Holochilus magnus* available in North American collections. Because we were unable to detect any qualitative or quantitative differences between fossil and Recent material, we concluded that these taxa are conspecific. The species, for which *molitor* is apparently the oldest available name, shares some derived attributes with members of the genus *Holochilus*, but differs strikingly in other traits.

In this report we document our inference that *Hesperomys molitor* and *Holochilus magnus* are conspecific, and we diagnose a new genus to contain them. We describe comparisons between the new genus and *Holochilus* (sensu stricto), provide phylogenetic analyses of morphological and karyotypic data, and evaluate the hypothesis that these taxa, together with *Pseudoryzomys*, *Zygodontomys*, and the oryzomyine genera of Hershkovitz (1944, 1960), form a monophyletic group. Finally, we summarize available natural history information from Recent populations of *molitor* and discuss the paleoecological implications of the Lagoa Santa fossils.

ACKNOWLEDGMENTS

We are grateful to the curators and technicians of the museums listed below (in Ma-

terials and Methods) for their hospitality while we visited their collections, and for their patience and generosity in extending many loans of scarce material. Tove Hatting, Hans Baagøe, Frits Braestrup, and Mogens Andersen of the Universitets Zoologisk Museum enthusiastically supported our studies of Lund's collections, and their careful stewardship of this important research resource merits high praise.

All of the drawings in this report are the work of Pat Wynne, whose graceful renditions of teeth and skulls clarify many essential details of our comparisons. Peter Goldberg photographed the skulls and tooththrows, and printed figure 17 from a negative in the AMNH Department of Mammalogy archives. The portrait of Lund reproduced in figure 1 was provided by Tove Hatting.

Nancy Simmons ran the phylogenetic analyses of our data and generously consented to read yet another long manuscript about rats. We also thank Phil Myers, Jim Patton, and Scott Steppan for their critical comments, including those with which we did not agree. Any remaining errors or annoying idiosyncrasies are, of course, our own.

MATERIALS AND METHODS

SPECIMENS: The specimens examined in the course of this study are deposited in the collections of the American Museum of Natural History, New York (AMNH); the Field Museum of Natural History, Chicago (FMNH); the Museum of Comparative Zoology at Harvard University, Cambridge (MCZ); the Museum of Michigan State University (MSU); the University of Michigan Museum of Zoology (UMMZ); the National Museum of Natural History, Washington, D.C. (USNM); and the Universitets Zoologisk Museum, Copenhagen (UZM).

MEASUREMENTS, AGE CRITERIA, AND ANATOMY: Total length (TL), length of tail (LT), and length of hindfoot (including claws, HF) were recorded from specimen tags; undistorted hindfeet were also remeasured on dry study skins to check the accuracy of values recorded by the collector. Length of head-and-body was obtained by subtracting LT from TL.

Cranial and dental dimensions were mea-

sured with dial calipers and recorded to the nearest 0.05 mm, but values reported below are rounded to the nearest 0.1 mm. The following measurements were defined and illustrated by Voss (1991): Condylar-incisive length (CIL), length of the diastema (LD), crown length of the upper molar series (LM), breadth of M1 (BM1), length of the incisive foramina (LIF), breadth of the rostrum (BR), breadth of the palatal bridge (BPB), breadth of the zygomatic plate (BZP), least interorbital breadth (LIB), depth of the incisors (DI), and length of the orbital fossa (LOF). Zygomatic breadth (ZB) is measured across the squamosal zygomatic processes (Voss, 1988: fig. 1). Crown length of the lower molar series (Lm1–m3) only appears in the caption to figure 6 of this report.

The term “adult” here denotes animals with completely erupted dentitions regardless of apparent sexual maturity. “Older specimens” or “older adults” refer to animals with well-worn molars.

Unless otherwise noted or explained, our anatomical terminology follows Reig (1977), Carleton (1980), Voss, (1988), and Carleton and Musser (1989).

ARCHIVES: Fieldnotes quoted or cited in this report are conserved in the archives of the Department of Mammalogy of the American Museum of Natural History, as are the photographic records of the 1962–63 Uruguayan expedition (from which fig. 17 is reproduced).

LUNDOMYS, NEW GENUS

TYPE SPECIES: *Hesperomys molitor* Winge, 1887.

ETYMOLOGY: For Peter Wilhelm Lund (fig. 1), whose excavations of caves near Lagoa Santa provided the first detailed record of an extinct mammalian fauna from South America. Unlike many professional fossil hunters obsessed with large specimens for public display, Lund was an academically accomplished biologist who studied both fossil and Recent species to test hypotheses about the history of life. As a consequence, Lund's collections are extraordinarily diverse, especially in small mammals, and provide a unique resource for understanding Quaternary extinctions in South America (Voss and Myers,



Fig. 1. Peter Wilhelm Lund (1801–1880), whose lonely dedication and prodigious labors to document the prehistoric diversity of Brazilian mammals we acknowledge with a genus named in his honor.

1991). Lund's scientific career and the impact of his research on the development of South American paleontology are described by Paula Couto (1950), Hattin (1980), and Simpson (1984).

DIAGNOSIS AND DESCRIPTION: As for the single included species, below.

Lundomys molitor (Winge, 1887)

Hesperomys molitor Winge, 1887: 14.

Oryzomys molitor: Trouessart, 1898: 528.

Holochilus magnus Hershkovitz, 1955: 657.

Calomys molitor: Hershkovitz, 1962: 123.

Holochilus molitor: Massoia, 1980: 282.

TYPE MATERIAL: We designate as lectotype the large cranial fragment (fig. 2) illustrated by Winge (1887) and labeled in his hand, consisting of the facial skeleton and anterior portion of the braincase of a young adult animal; the specimen is deposited in the pale-

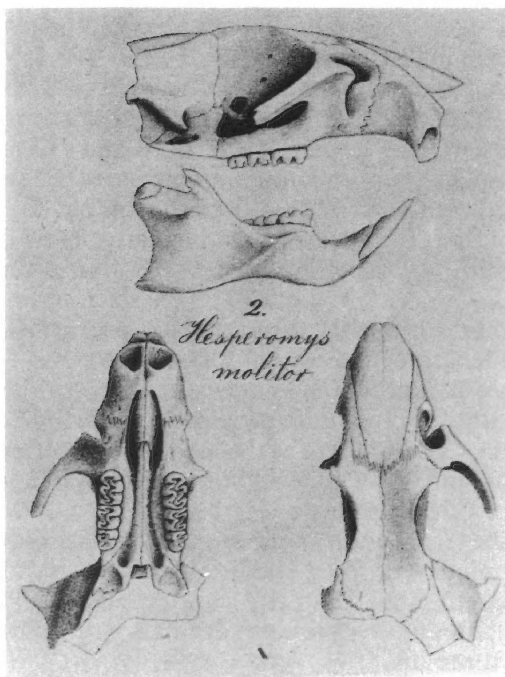


Fig. 2. The lectotype of *Lundomys molitor* with its label (both about $\times 1.5$, left), and Winge's (1887) illustration (right).

ontological collections of the Universitets Zoologisk Museum but does not have a catalog number. The lectotype was collected from the cave chamber that Lund designated "Lapa da Escrivania Nr. 5," near Lagoa Santa, Minas Gerais, Brazil. Two additional, uncataloged specimens in the Universitets Zoologisk Museum (also labeled by Winge) are hereby designated paralectotypes; these consist of another large skull fragment and an isolated maxillary tooththrow, both from Lapa da Escrivania Nr. 5. A complete mandible (fig. 2, right) from another cave, Lapa da Serra das Abelhas, was also part of Winge's hypodigm but does not represent the same species as the cranial material from Lapa da Escrivania Nr. 5; its taxonomic allocation will be the topic of a future report.

REMARKS: Comparisons between Recent specimens and fossils are inevitably limited by the anatomical incompleteness of the latter. The type series of *Lundomys molitor* consists of just three fragmentary specimens, but these are sufficient to document the identity

of this taxon with Recent material hitherto identified as *Holochilus magnus* in qualitative characters of the nasal bones, interorbital region, zygomatic arch, zygomatic plate, incisive foramina, palatal bridge, orbital and alisphenoid foramina, and maxillary dentition (compare fig. 2 with figs. 3A and 4A, and fig. 5A with 5B). These qualitative likenesses, together with completely overlapping measurement variation (table 1) compel us to conclude that *molitor* and *magnus* are conspecific. Characters determinable only from Recent material are therefore included in the diagnosis, description, and comparisons that follow.

EMENDED DIAGNOSIS: Very large rodents of the muroid subfamily Sigmodontinae (sensu Carleton and Musser, 1984) with tail longer than head-and-body; hindfeet large, conspicuously webbed, with long fringes of silvery hairs along plantar margins, without unequal tufts, and with only five small plantar pads; skull with narrow interorbit and convergent zygoma; broad zygomatic plate with spinous

anterodorsal process; posterior wall of orbit without prominent vertical ridge along frontal-squamosal suture; tegmen tympani not connected to posterior suspensory process of squamosal; subsquamosal fenestra patent and subequal to postglenoid foramen; incisive foramina long, extending posteriorly to or between molar alveoli; palate long and narrow with prominent posterolateral pits; alisphenoid strut absent; carotid circulation without stapedial contribution to facial supply; molar dentition bunodont; labial and lingual folds not interpenetrating; unworn M1 and M2 with small mesolophs; M3 shorter than M2; unworn m1 and m2 usually with small mesolophids; superior and inferior masseteric ridges of mandible converging as open chevron; capsular process of lower incisor alveolus inconspicuous; basihyal without entoglossal process; first rib articulating with transverse processes of seventh cervical and first thoracic vertebrae; 12 ribs; gall bladder absent.

MORPHOLOGICAL DESCRIPTION: Very large rats with huge hindfeet and long tails (table 2). Body pelage long, dense, and soft; clear yellow-brown along sides, near Clay Color (Smithe, 1975–1981: 123B), but darker dorsally from concentration of glossy, dark brown guard hairs; paler ventrally, near Warm Buff (op. cit.: 124), but the bases of ventral hairs gray. Ears small and well provided with short, brownish or yellowish fur, not contrasting sharply with fur of head and nape. Mystacial, superciliary, genal, submental, interramal, and carpal vibrissae present; mystacial vibrissae short, not extending posteriorly behind pinnae when laid back against head. Manus covered dorsally with short, pale hairs, without tufts of long ungual hairs at bases of claws (which therefore appear naked); plantar surface hairless and densely squamate, with two large carpal pads and three very small interdigital pads. Pes covered dorsally with short, pale hairs; without ungual tufts of longer hairs (claws naked); dense fringes of long, silvery hairs present along medial plantar margins of metatarsus and digits I and II, and along lateral plantar margins of digits IV and V; plantar surface hairless and densely squamate, with one metatarsal and four very small interdigital pads (hypothenar pad absent); claw of digit I extends at least to middle of

TABLE 1
Sex and Craniodental Measurements (mm) of Adult *Lundomys molitor* from Lagoa Santa (Brazil) and from Uruguay

Lagoa Santa			Uruguay ^a
	The lecto-type	Another specimen	
Sex			5 males, 5 females 2 sex unknown
CIL			40.8 ± 3.0 (35.2–45.0) 11
LD	10.6	11.7	11.7 ± 1.2 (9.7–13.5) 12
LM	8.0	8.5	8.3 ± 0.1 (8.0–8.5) 12
BM1	2.5	2.6	2.6 ± 0.1 (2.5–2.8) 12
LIF	8.4	9.8	8.7 ± 0.6 (7.7–9.8) 12
BR	7.9	8.0	7.3 ± 0.6 (6.2–8.2) 12
BPB	3.3	3.5	3.2 ± 0.5 (2.4–4.0) 10
BZP	3.8	4.8	4.5 ± 0.4 (3.6–5.1) 12
LIB	5.4	5.3	5.1 ± 0.3 (4.7–5.5) 10
ZB			24.3 ± 1.5 (21.5–26.1) 10
DI		2.8	2.5 ± 0.3 (2.1–2.8) 12
LOF	14.2		15.5 ± 1.1 (13.5–17.2) 11

^a The mean, standard deviation, observed range (in parentheses), and sample size are provided for measurements of: AMNH 206363, 206364, 206366, 206368, 206380, 206381, 206392, 206393; FMNH 29255, 29257, 29258 (the type of *Holochilus magnus*), 29260–29263; MCZ 26944; USNM 259641.

phalange 1 of digit II; claw of digit V extends to end of phalange 1 of digit IV; interdigital webs present and well developed, extending beyond first phalanges among digits II, III, and IV. Tail unicolored (dark), sparsely haired (the epidermal scales clearly visible), and without a tuft or pencil of longer hairs at tip. Mammae eight in inguinal, abdominal, postaxial, and pectoral pairs.

Skull with blunt, massive rostrum flanked by deep zygomatic notches; interorbital region very narrow, with sharp but not beaded supraorbital margins; braincase with low scar of temporalis origin on each side but without well-developed temporal crests; posterior wall of orbit without a prominent vertical ridge along frontal-squamosal suture; lambdoidal and nuchal crests well developed in older adults. Zygomatic plate broad, with concave anterior margin and spinous anterodorsal process; zygomatic arches strong and convergent anteriorly (widest across squamosal roots); jugal present and always separating maxillary and squamosal zygomatic process-

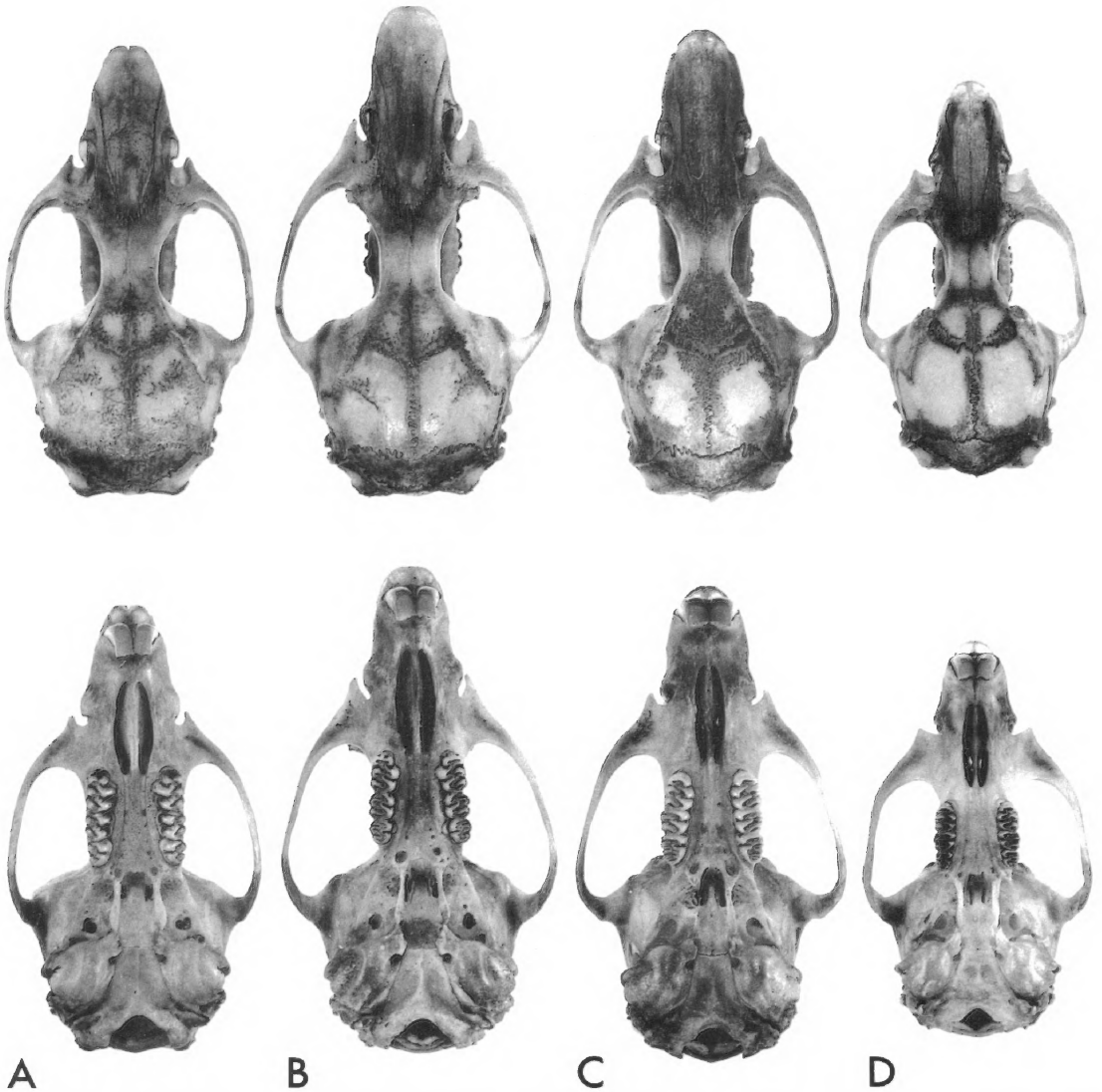
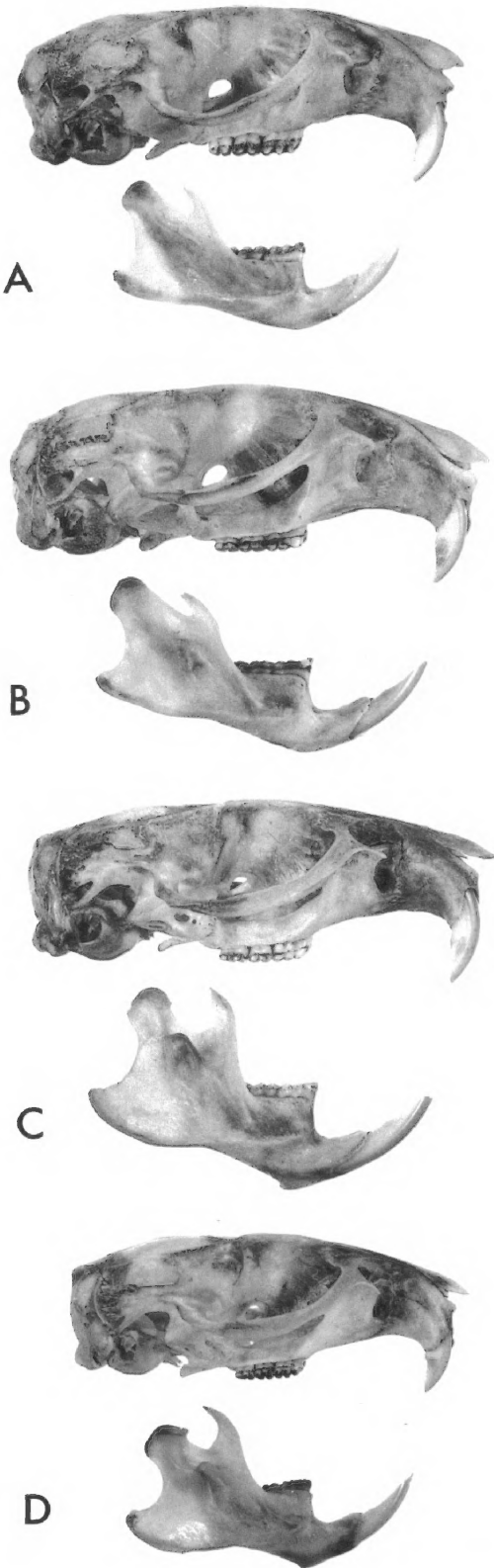


Fig. 3. Dorsal and ventral views of skulls ($\times 1.5$) of *Lundomys* and *Holochilus*. A, young adult *Lundomys molitor* (AMNH 206364, about the same age as the lectotype); B, an older adult (AMNH 206393); C, *Holochilus brasiliensis* (AMNH 206369); D, *Holochilus sciureus* (AMNH 210263).

es. Incisive foramina long, extending posteriorly to or between molar alveoli; palatal bridge long and narrow, with prominent posterolateral pits; parapterygoid fossae each about as wide as mesopterygoid fossa, moderately recessed above level of palate; roof of mesopterygoid fossa apparently completely ossified or with very small sphenopalatine vacuities flanking basisphenoid-presphenoid suture (but mesopterygoid region damaged in most available specimens). Alisphenoid strut absent (buccinator-masticatory and acces-

sory oval foramina confluent). Carotid circulation with facial supply from internal anastomosis of internal carotid artery, not from stapedial artery (pattern 3 of Voss, 1988). Tegmen tympani not connected to posterior suspensory process of squamosal; dorsolateral wall of braincase above auditory bulla perforated by subequal postglenoid foramen and subsquamosal fenestra. Auditory bullae globular (with short and narrow bony eustachian tubes); periotic broadly exposed posteromedially between ectotympanic and



basioccipital but not extending anteriorly to carotid canal.

Coronoid process of mandible about level with condyle; angular process not produced posteriorly much beyond condyle; superior and inferior masseteric crests converging as open chevron (not tightly compressed to form a single anterior ridge); capsular process of lower incisor alveolus an inconspicuous swelling below base of coronoid process. Basihyal without entoglossal process.

Upper incisors opisthodont, with smoothly rounded (not faceted), bright yellow-orange enamel bands. Upper and lower molars bunodont; labial and lingual cusp margins rounded (not angular). Anterocone of unworn M1 weakly divided into subequal labial and lingual lobes by shallow anteromedian flexus; anteroloph present but small on unworn M1, well developed on M2 and M3; shallow protoflexus present on unworn M2; small mesoloph always present on M1 and M2 (but never fused with mesostyle on labial cingulum), usually absent from M3; minute posteroloph present on newly erupted upper molars but quickly obliterated by wear; all upper molars with three roots. Anteroconid of m1 entire (not divided by anteromedian flexid), but enclosing large enamel pit; minute anterolophids present on all unworn lower molars; small mesolophids present on unworn m1 and m2, absent from m3; discrete posterolophids present and persistent on m1 and m2, usually absent on m3; m1 with three or four roots, m2 and m3 with two roots each.

Tuberculum of first rib articulating with transverse processes of seventh cervical and first thoracic vertebrae; second thoracic vertebra with greatly elongated neural spine; axial skeletal counts (from nine specimens) including 12 ribs, 19 thoracolumbar vertebrae, 4 sacrals, and 35 or 36 caudals; entepicondylar foramen of humerus absent.

Stomach unilocular and strictly hemiglandular, with no leftward extension of glandular epithelium into corpus; gall bladder absent (Voss, 1991: table 4); other visceral characters undetermined.



Fig. 4. Lateral views of skulls and mandibles (both $\times 1.5$) of *Lundomys* and *Holochilus*. Specimens are the same as those in figure 3.

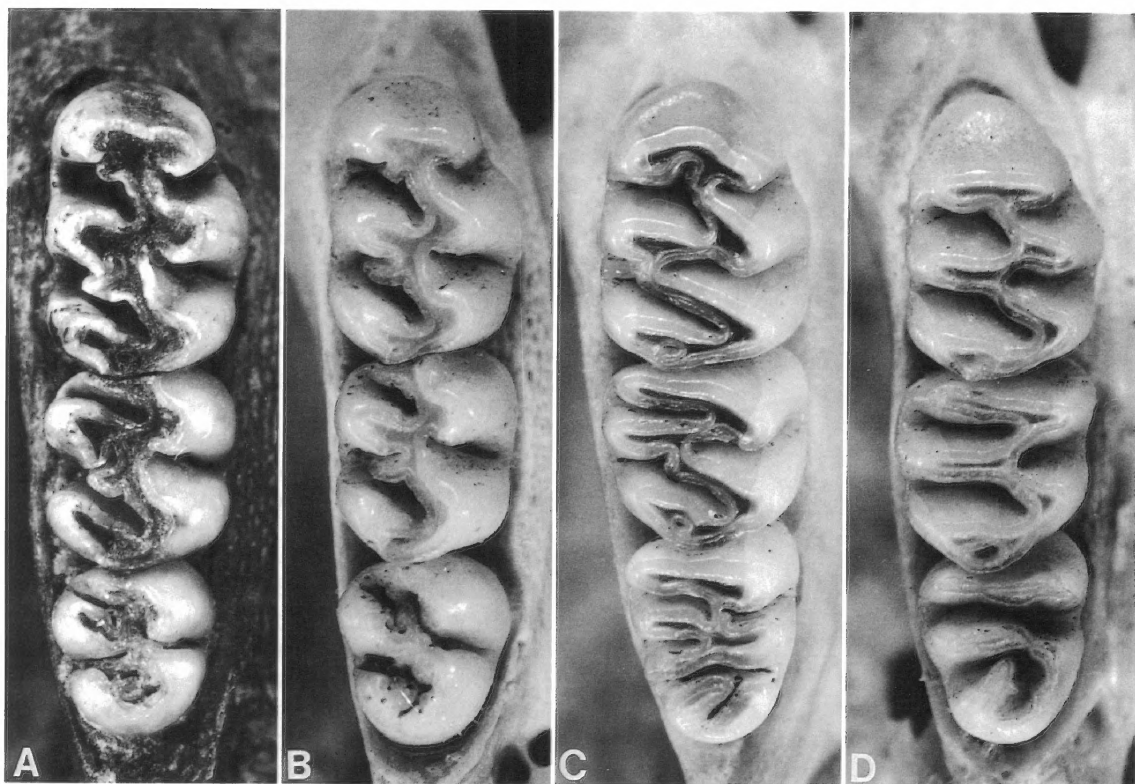


Fig. 5. Right upper molars of *Lundomys* and *Holochilus*. A, the lectotype of *Lundomys molitor* (LM = 8.0 mm); B, a Recent specimen (AMNH 206388, LM = 8.3 mm); C, *Holochilus brasiliensis* (AMNH 206372, LM = 8.1 mm); D, *Holochilus sciureus* (AMNH 134703, LM = 7.3 mm).

KARYOTYPES: Five specimens (two males and three females) collected along the Ivai River near Tupanciretã, Rio Grande do Sul, Brazil (28°56'S, 53°40'W) were karyotyped by Freitas et al. (1983), who reported a diploid number of 52 and a fundamental number of 58; the biarmed autosomes consist of three pairs of large metacentrics and one small metacentric pair; the X is submetacentric, the Y is metacentric.

DISTRIBUTION: All Recent specimens of *Lundomys molitor* of which we are aware have been collected in Uruguay or in the adjacent Brazilian state of Rio Grande do Sul (fig. 7). Redford and Eisenberg (1992) stated that the species occurs in Argentina and mapped a locality in the delta of the Paraná; we have seen no specimens or other published records of Recent material from that country, but Bond and Massoia (1981) and Lezcano et al. (1992) reported late Pleistocene material from the province of Buenos Aires.

Herskovitz (1955) suggested that a fluid-preserved specimen from Lagoa Santa identified by Winge (1887) as *Sigmodon vulpinus* (= *Holochilus brasiliensis*) might actually be an example of *Holochilus magnus* (= *Lundomys molitor*). We examined the specimen in question (UZM 399), which has since been partially skeletonized, and determined that the cranium and dentition are unambiguously those of *H. brasiliensis*. The type locality of *L. molitor* is therefore considerably removed from the known geographic range of Recent populations (fig. 7).

SPECIMENS EXAMINED: **Brazil**—*Minas Gerais*, near Lagoa Santa (the lectotype and two paralectotypes, in the Universitets Zoologisk Museum, Copenhagen). **Uruguay**—*Canelones*, Bañado de Tropa Vieja, 36 km E Montevideo (AMNH 206363–206366); *Lavalleja* (formerly *Minas*), Paso de Averías, Río Cebollati (FMNH 29255, 29257, 29258; USNM 259641); *Soriano*, 3 km E Cardona (AMNH

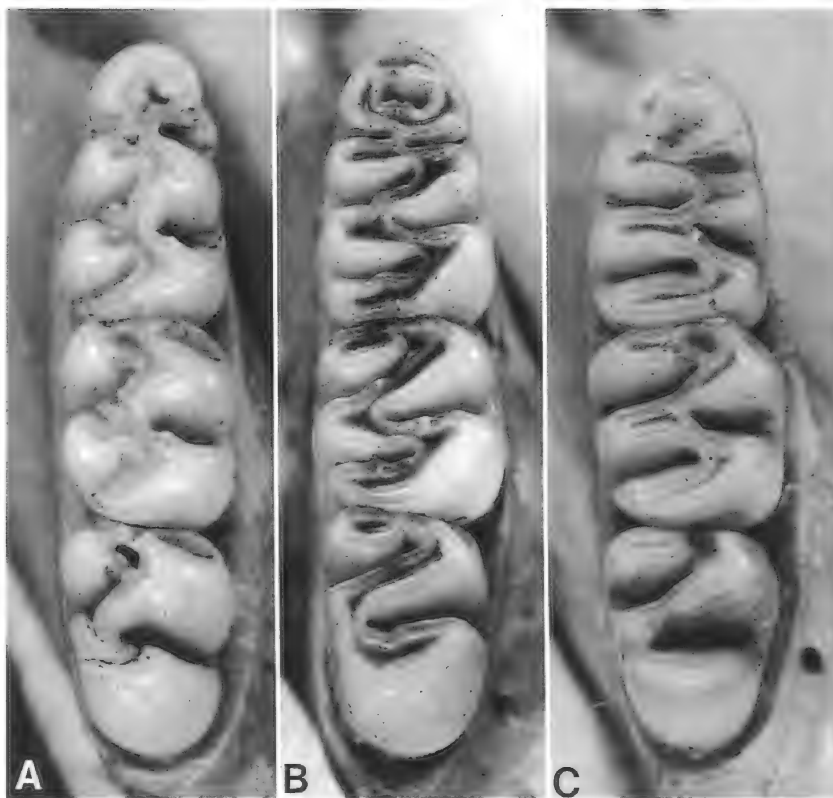


Fig. 6. Right lower molars of *Lundomys* and *Holochilus*. A, *Lundomys molitor* (AMNH 206388, Lm1-m3 = 8.7 mm); B, *Holochilus brasiliensis* (AMNH 206372, Lm1-m3 = 8.8 mm); C, *Holochilus sciureus* (AMNH 134703, Lm1-m3 = 7.5 mm).

206368, 206373, 206380, 206381, 206388); Trienta y Tres, 8 mi E Trienta y Tres (FMNH 29260, 29261, 29263; MCZ 26944), and Rio Olimar Chico, 25 km WSW Trienta y Tres (AMNH 206392, 206393). Total = 22.

COMPARISONS WITH *HOLOCHILUS*

Lundomys molitor resembles species of *Holochilus* in numerous characters, including derived aspects of external, craniodental, and visceral morphology. Differences in other anatomical traits are substantial, however, and suggest that each genus represents an evolutionarily distinct lineage with a unique combination of adaptations for diet and locomotion. In these comparative accounts we describe morphological similarities and differences that provide data for subsequent analyses of phylogenetic relationships and/or evidence of ecological specializations.

We emphasize at the outset the preliminary

and exploratory nature of these exercises. Specimens of *Lundomys molitor* are not abundant, and with only the small samples at hand it is possible that we have underestimated the variability of this taxon. Additional complexity is introduced by character variation within *Holochilus* that clearly merits recognition at the species level. Whereas Hershkovitz (1955) referred all of the named forms of *Holochilus* (in the strict sense of this report) to *H. brasiliensis*, we provisionally accept Massoia's (1981) argument that *brasiliensis* (including *darwini* and *vulpinus*) should be restricted to populations of large rats with unexpanded paracones and vestigial mesolophs on M1 and M2. This distinctive species ranges from northeastern Argentina (cf. Massoia, 1974: fig. 1) throughout Uruguay to the southeastern states of Brazil (including parts of Minas Gerais and Bahia; Massoia, 1981). The remaining geographic populations of *Holochilus*, for which the old-

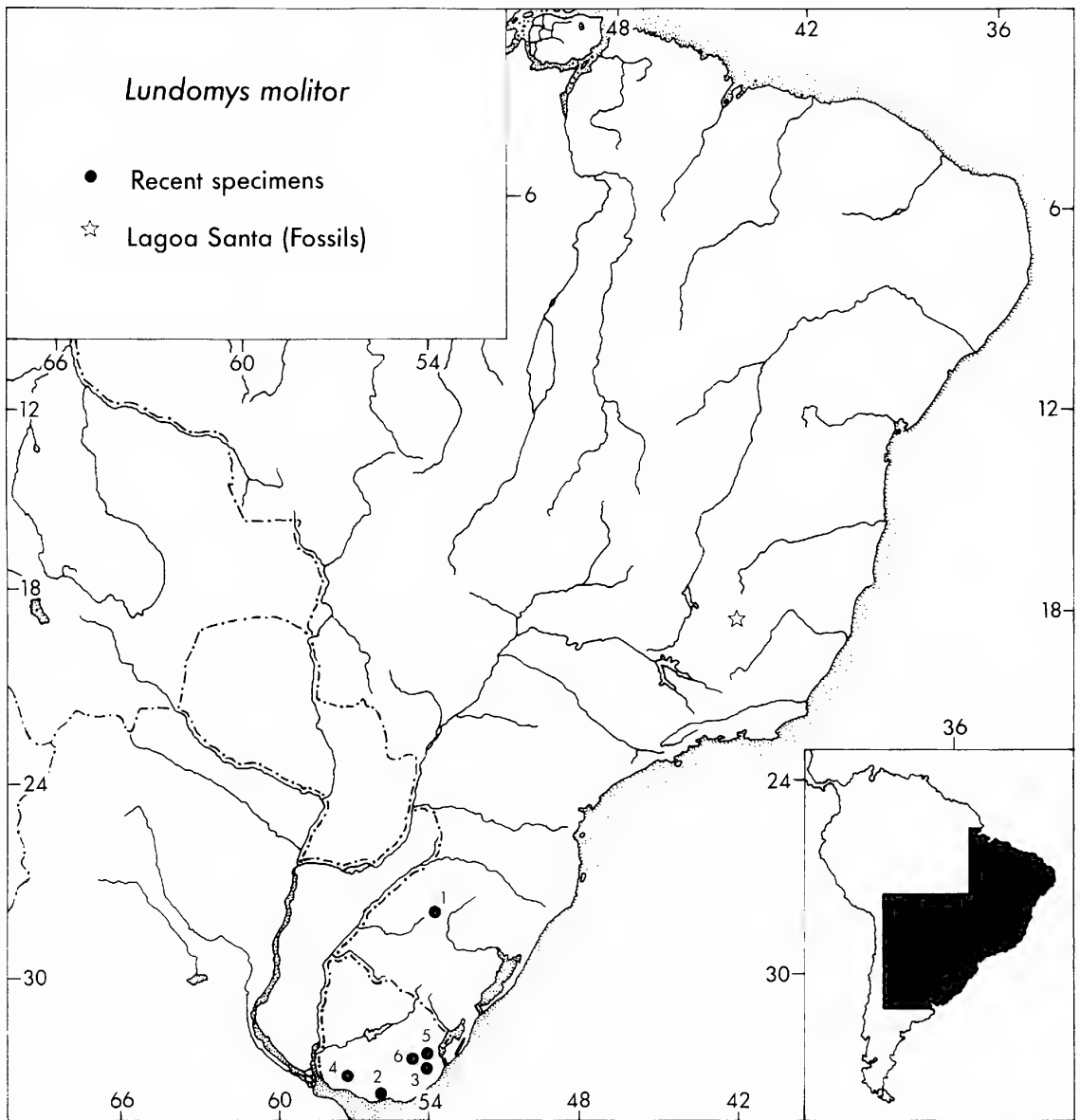


Fig. 7. Geographic distribution of Recent and fossil samples of *Lundomys molitor*. Recent collection localities with unpunctuated geographic coordinates (degrees and minutes S latitude / W longitude, if known) are numbered as follow: 1, BRAZIL, Rio Grande do Sul, Tupanciretã (2856/5340) (reported by Freitas et al., 1983; specimens not examined by us); 2, URUGUAY, Canelones, Bañado de Tropa Vieja (3447/5552); 3, URUGUAY, Lavalleja, Paso de Averías (3336/5419); 4, URUGUAY, Soriano, 3 km E Cardona; 5, URUGUAY, Trienta y Tres, 8 km E Trienta y Tres (3314/5423) and 6, 25 km WSW Trienta y Tres.

est unambiguously available name appears to be *sciureus* Wagner 1842, comprise a morphologically cohesive assemblage of smaller animals with expanded paracones but no mesolophs on M1 and M2. (These and other characters distinguishing *H. sciureus* from *H.*

brasiliensis are explained in greater detail below.) We acknowledge that karyotypic comparisons have revealed substantial divergence among some geographic samples of *sciureus*-like rats (e.g., those currently referred to *chacarius* and *venezuelae*; see Vidal

TABLE 2
Summary Statistics^a for External Measurements (mm) of Adult Specimens of *Lundomys molitor* and Species of *Holochilus*

Species	Length of head-and-body	Length of tail	Length of hindfoot
<i>Lundomys molitor</i> ^b	193 ± 22 (160–230) 10	235 ± 19 (195–255) 10	62 ± 3 (58–68) 12
<i>Holochilus brasiliensis</i> ^c	193 ± 14 (167–211) 10	198 ± 10 (183–214) 10	54 ± 2 (51–56) 10
<i>Holochilus sciureus</i> ^d	164 ± 18 (123–193) 33	150 ± 16 (115–178) 33	39 ± 3 (35–46) 33

^a The sample mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size.

^b The sample identified in the footnote to table 1.

^c Specimens from Uruguay, Depto. Soriano: AMNH 206369, 206372, 206374–206379, 206382, 206383.

^d Specimens from Paraguay, Depto. Presidente Hayes: UMMZ 125997–126004, 126074–126078, 133971–133974, 133976, 133977, 133979, 133980, 166197–166206, 166208, 166209.

et al., 1976; and Aguilera and Perez-Zapata, 1989), but the morphological data at hand do not yet suggest clearcut subdivisions of this complex.

Skins and skulls of *Holochilus brasiliensis* and of the *H. sciureus* complex (for brevity, hereafter referred to simply as *H. sciureus*) that we examined for these comparisons include large series from the AMNH, FMNH, and USNM collections. Fluid-preserved specimens (which are much less numerous) are cited by museum catalog number in the descriptive accounts below.

EXTERNAL MORPHOLOGY

Size and general aspect: That a systematic mammalogist as astute as Sanborn (1929) did not recognize another taxon within the series of Uruguayan specimens he identified as *Holochilus vulpinus* (= *H. brasiliensis*) is eloquent testimony to the close external resemblance between *Holochilus* and *Lundomys*. Species of *Holochilus* and *Lundomys molitor* are all large rats (table 2) whose tawny or brownish dorsal pelage is grizzled or streaked with darker guard hairs. Populations of *H. sciureus* from tropical lowland habitats have short, close fur, but at temperate latitudes (as in Uruguay) both *H. brasiliensis* and *L. molitor* have dense, soft, luxurious pelts. The ears are small and well furred in each genus, the mystacial vibrissae are short (not extending behind the pinnae when folded back along the cheeks), and tails are sparsely haired with conspicuous annuli of coarse scales. Other external traits merit closer attention.

External proportions and hindfeet: Rela-

tive to the combined length of head and body, the appendages of *Lundomys molitor* are larger than those of *Holochilus* species (table 2). The tail provides a particularly conspicuous morphometric contrast, averaging much longer than head-and-body in *Lundomys*, about as long as head-and-body in *H. brasiliensis*, and consistently shorter than head-and-body in *H. sciureus*. Comparisons of relative length of the hindfoot yield the same taxonomic ranking, but qualitative aspects of this organ are more informative.

In both *Lundomys* and *Holochilus*, the three middle digits of the hindfoot (II, III, and IV) are much longer than the outer digits (I and V); the claw of digit I does not extend more than half the length of the first phalange of II, while the claw of V does not extend beyond the first interphalangeal joint of IV. These unremarkable digital proportions are widespread among other Neotropical muroids, including such strictly terrestrial (non-arboreal and nonaquatic) species as *Zygodontomys brevicauda* (Voss, 1988).

The dorsal pelage of the hindfoot in both genera is close and sparse, and the claws appear naked because they are not concealed by ungual tufts of longer hairs. (Most other Neotropical muroids have well-defined tufts of long, curved hairs rooted at the bases of the claws; when present, these ungual tufts are as long as or longer than the claws they wholly or partially conceal.) Another noteworthy aspect of the pelage of the hindfoot is the development of what may be termed “natatory fringes” along some of the plantar margins. These are formed by longer hairs with a silvery cast, although tinged with the

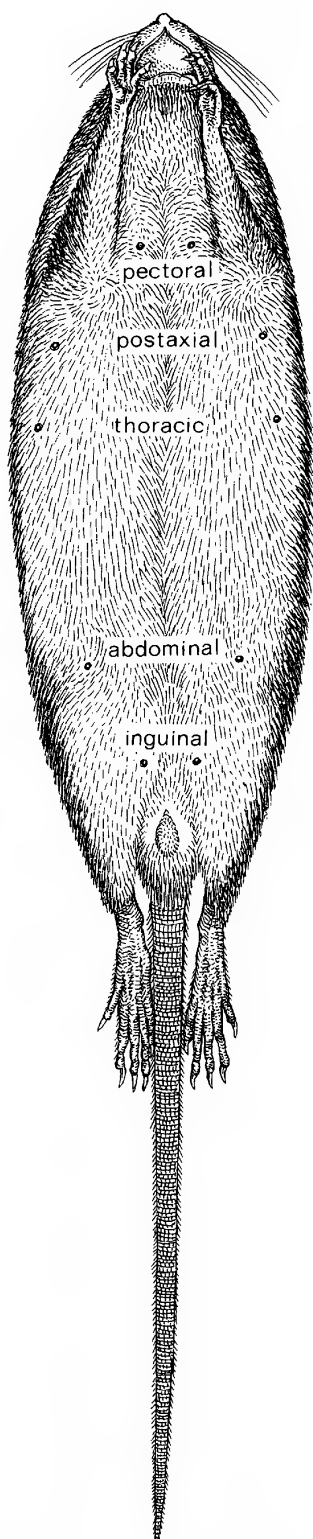


Fig. 8. Anatomical loci of mammary pairs discussed in the text.

predominant pigment (usually yellowish or brownish) of the dorsal pelage of the foot. In *Lundomys molitor*, stiff, dense natatory fringes are present along the medial plantar margins of the metatarsus and digits I and II, and along the lateral plantar margins of digits IV and V; the lateral metatarsus and other digital plantar margins are unfringed. Natatory fringes are present but only weakly developed in *Holochilus brasiliensis* and *H. sciureus*.

In both *Lundomys* and *Holochilus*, the plantar epithelium is smooth over the heel, but the remainder (from about the level of the thenar pad nearly to the ends of the digits, and including the webs) is densely covered with small tubercles that have the appearance of scales; this uniformly squamate surface is interrupted only by five or six small plantar pads (Sierra de Soriano, 1965: lámina III). The thenar (medial metatarsal) pad and four interdigital pads are invariably present; a very small hypothenar pad is occasionally present in specimens of *H. sciureus* (often unilaterally), but not in any examples of *H. brasiliensis* or *Lundomys molitor* that we examined.

The hindfeet are webbed in both *Holochilus* and *Lundomys*. Although present between all adjacent digits, webs are best developed between II and III and between III and IV. Webs between these middle digits extend only to the ends of the first phalanges in both species of *Holochilus*, but in *Lundomys* the webs extend well beyond the first interphalangeal joint (especially between digits III and IV; Sierra de Soriano, 1965: lámina III).

Mammae: Two skins of adult female *Lundomys molitor* (AMNH 206380, 206392) have eight mammae in four pairs, one inguinal, one abdominal, one postaxial, and one pectoral (see fig. 8 for a diagram of mammary loci). Hershkovitz (1955) reported ten mammae for *Holochilus*, but mammae number is variable in that genus. All of the lactating female specimens of *H. brasiliensis* that we examined (e.g., AMNH 206369, 206372, 206379; MSU 17892, 17893) have eight mammae in the same anatomical pattern as described for *L. molitor*, but geographic samples of *H. sciureus* have either eight or ten teats (table 3). Populations of *H. sciureus* with ten mammae have paired thoracic teats in

addition to the usual complement of inguinal, abdominal, postaxial, and pectoral pairs.

CRANIUM AND MANDIBLE

Zygomatic and orbital morphology: In both *Lundomys* and *Holochilus* the zygomatic plate is very broad and a blunt spinous process extends its free dorsal edge to define a deep zygomatic notch on each side of the rostrum. The stout zygomatic arches are widest across their squamosal roots and converge anteriorly. In specimens of *Lundomys*, the jugal is small but consistently present and separates the zygomatic processes of the maxillary and squamosal bones. In both *Holochilus brasiliensis* and *H. sciureus*, however, the jugal is smaller and irregularly formed, such that the maxillary and squamosal are often in contact along the midportion of the zygomatic arch.

The anterior interorbital region in both *Lundomys* and *Holochilus* is very narrow and basically hourglass-shaped with sharp dorsolateral margins, but the posterior frontals of *Holochilus* are usually produced as raised supraorbital beads (especially prominent in older specimens). The dorsolateral margins of the posterior frontals sometimes form small shelves in *Lundomys* but raised beads are absent even in the oldest specimens we examined.

A vertical bony ridge is developed on the posterior wall of the orbit in *Holochilus*, extending approximately from the supraorbital bead previously described to a point just above the zygomatic root of the squamosal; the ridge usually overlaps the line of frontal-squamosal contact, and obscures the suture from lateral view (fig. 9B). As with other osseous features associated with muscular origins, the development of the postorbital ridge appears to vary with age and size. It is better defined in mature specimens than in younger animals, and is better expressed in larger-bodied populations (e.g., of *H. brasiliensis*) than in smaller-bodied ones (e.g., some geographic samples of the *H. sciureus* complex). A distinct postorbital ridge is never present in *Lundomys* although a low scar posterior to the frontal-squamosal suture of some specimens may be homologous; accordingly, the suture is plainly visible in lateral view (fig. 9A).

TABLE 3
Mammæ Counts from Geographic Samples of the *Holochilus sciureus* Complex

Samples ^a	Mammæ
Bolivia, Depto. Beni	
AMNH 210274	ten
210275	ten
210303	ten
210305	ten
Brazil, Edo. Amazonas	
AMNH 37083	eight
92280	eight
92730	eight
93539	eight
Brazil, Edo. Goiás	
AMNH 134693	eight
134699	eight ^b
Colombia, Depto. Meta	
AMNH 136322	ten ^c
142121	ten
142122	ten
Paraguay, Depto. Pres. Hayes	
UMMZ 126001	ten
166197	ten
166201	ten
166205	ten
Peru, Depto. Loreto	
AMNH 76278	eight
76281	eight
76283	eight
76288	eight
76289	eight
76290	eight
Venezuela, Edo. Trujillo	
USNM 372662	ten
372663	ten
372664	ten

^a Only adult specimens with large mammæ surrounded by well-defined areolæ are listed for each sample.
^b Collector's label notes only six mammæ.
^c Collector's label notes only eight mammæ.

Palate and palatal foramina: The incisive foramina of the diastemal palate consistently extend posteriorly to or between the molar alveoli in *Lundomys* (figs. 3A, 3B), but in *Holochilus* these openings are less extensive. In young adult *Holochilus* (with fully erupted but unworn maxillary dentitions), the foramina sometimes extend posteriorly between the molar alveoli but in older specimens the fo-

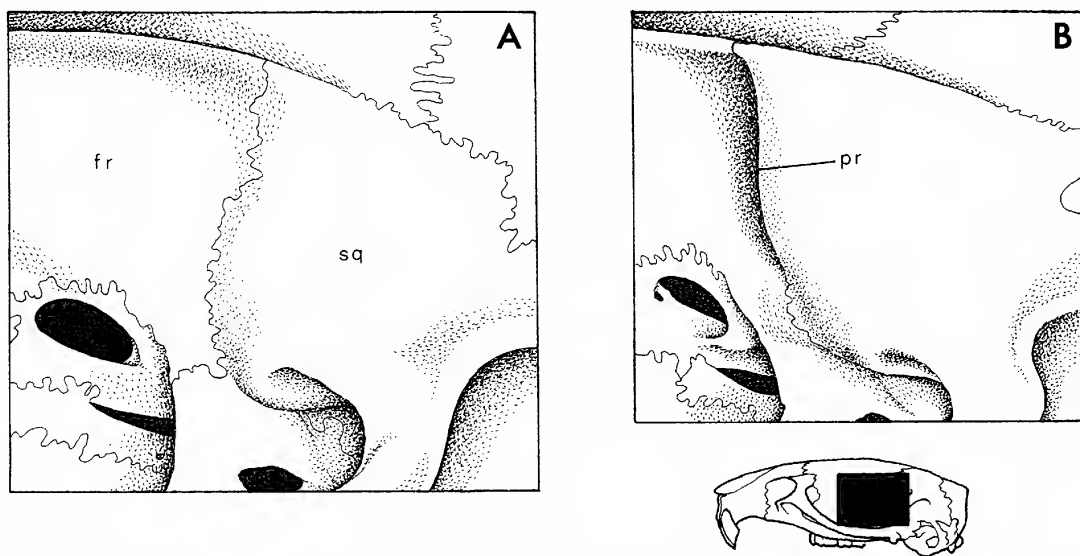


Fig. 9. Postorbital morphology. A, *Lundomys molitor* (AMNH 206393); B, *Holochilus brasiliensis* (AMNH 206369). The suture between the frontal (fr) and squamosal (sq) bones is not marked by any conspicuous relief in *Lundomys*, but a prominent bony fold (the postorbital ridge, pr) partially conceals this suture in mature specimens of *Holochilus*.

ramina always stop well short of the molar rows (figs. 3C, 3D).

The palatal bridge of *Lundomys* is unambiguously "long" in the sense defined by Hershkovitz (1962: 54) because it is produced posteriorly beyond the molar rows. Mature adult specimens of *Holochilus brasiliensis* also have long palates, but in some samples of *H. sciureus* the mesopterygoid fossa often extends to or slightly between the third molars. In both genera, paired posterior palatal foramina perforate the maxillary-palatine suture between the second molars, and prominent posterolateral palatal pits are present between the third molars and the mesopterygoid fossa. Small foramina of inconstant number and morphology are usually present in the shallow grooves that connect the posterior palatal foramina with the posterolateral palatal pits.

Alisphenoid strut: In all specimens of *Holochilus* examined, a stout strut of the alisphenoid separates the buccinator-masticatory foramen from the foramen ovale accessorius (fig. 10A). The alisphenoid strut is absent from all available specimens of *Lundomys* in which a single alisphenoid perforation represents the confluent buccinator-masticatory and oval foramina (fig. 10B).

Carotid circulation: The occurrence and conformation of certain foramina and other osteological features suggest that the facial (ophthalmic and internal maxillary) circulation is supplied by the internal carotid, not by the stapedia artery, in both *Lundomys* and *Holochilus*: (1) the stapedia foramen is absent or persists only as a tiny perforation in the petrotympanic fissure on the postero-medial surface of each auditory bulla; (2) the interior surfaces of the squamosal and alisphenoid are not marked by a vascular groove, and the sphenofrontal foramen is absent; (3) the posterior opening of the alisphenoid canal is absent or small and irregularly formed; and (4) the carotid canal (between the bulla and the basioccipital) is large, and an oblique internal groove crosses the roof of the parapterygoid fossa to join with the anterior opening of a short alisphenoid canal. The relationship of these skeletal traits to alternative patterns of cephalic arterial circulation is explained and illustrated by Voss (1988: fig. 18) and by Carleton and Musser (1989: figs. 20, 21).

Ear region and temporal foramina: The ectotympanic bullae of both *Lundomys* and *Holochilus* are globular capsules that appear neither very small nor grossly enlarged in comparisons with those of other Neotropical

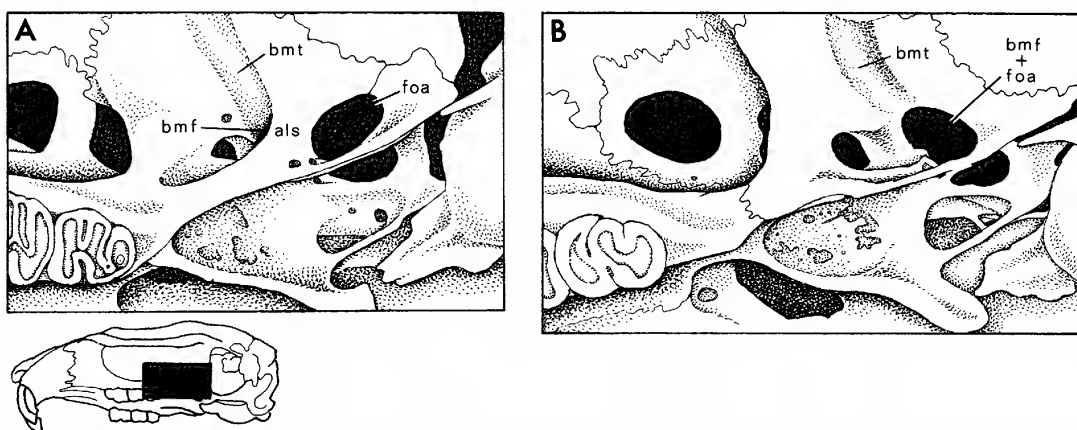


Fig. 10. Foramina and associated features of the alisphenoid bone. **A**, *Holochilus sciureus* (AMNH 210263); **B**, *Lundomys molitor* (AMNH 206393). A prominent strut of the alisphenoid (**als**) separates the buccinator-masticatory foramen (**bmf**) from the foramen ovale accessorius (**foa**) in *Holochilus*, but in *Lundomys* the strut is absent and the two foramina are confluent; a prominent groove or trough (**bmt**) marks the dorsal passage of the buccinator and masticatory nerves along the outer surface of the alisphenoid in both taxa.

muroids. The bullae are slightly more inflated in *Holochilus* than in *Lundomys*, however, as can be judged by the extent of periotic bone exposed between the ectotympanic and the basioccipital: only a narrow sliver of the periotic is visible on the ventromedial aspect of the bulla in *Holochilus*, but a broad wedge of the periotic is exposed in *Lundomys*. In neither genus does the periotic extend forward to reach the carotid canal, which is instead enclosed completely between the ectotympanic and basioccipital.

The anterior suspension of the auditory complex in both genera resembles that described for *Oryzomys palustris* by Voss (1993): the tegmen tympani projects anterodorsally from the bulla but is not connected to a posterior suspensory process of the squamosal. In lateral view, the tegmen tympani of *Lundomys* often appears to touch or overlap the posterior margin of the squamosal, but no posterior suspensory process is present and the bones are not pressed closely together in any specimens we examined. In most specimens of *Holochilus* the tegmen tympani is separated from the squamosal by an obvious (though sometimes narrow) gap.

The postglenoid foramen and the subsquamosal fenestra perforate the lateral wall of the braincase above the auditory bulla in both genera, but differences in the relative sizes of

these openings are noteworthy. The postglenoid foramen and subsquamosal fenestra (separated by a slender hamular process of the squamosal) are of approximately equal size in *Lundomys* and the central lumen of the braincase is visible through each. In both species of *Holochilus*, however, the postglenoid foramen is at least twice as large as the subsquamosal fenestra. In *H. brasiliensis* the subsquamosal fenestra is always distinct and patent, but in *H. sciureus* this opening is often occluded by an expanded hamular process or by an internal crest or septum of the periotic.

Mandible: The mandibular conformation of the two genera differs in numerous details (fig. 11). The coronoid process is small and angled posterodorsally in *Lundomys*, its tip slightly below or about level with the condyloid process, and the sigmoid notch is therefore narrow and elliptical. The coronoid process of *Holochilus* is much larger, oriented more nearly vertically, and projects well above the condyle, and the sigmoid notch is correspondingly broad and oval. The angular process of *Lundomys* does not extend posteriorly behind the condyle and the angular notch is a shallow concavity. By contrast, the angular process of *Holochilus* is produced well behind the condyle and the angular notch is much deeper.

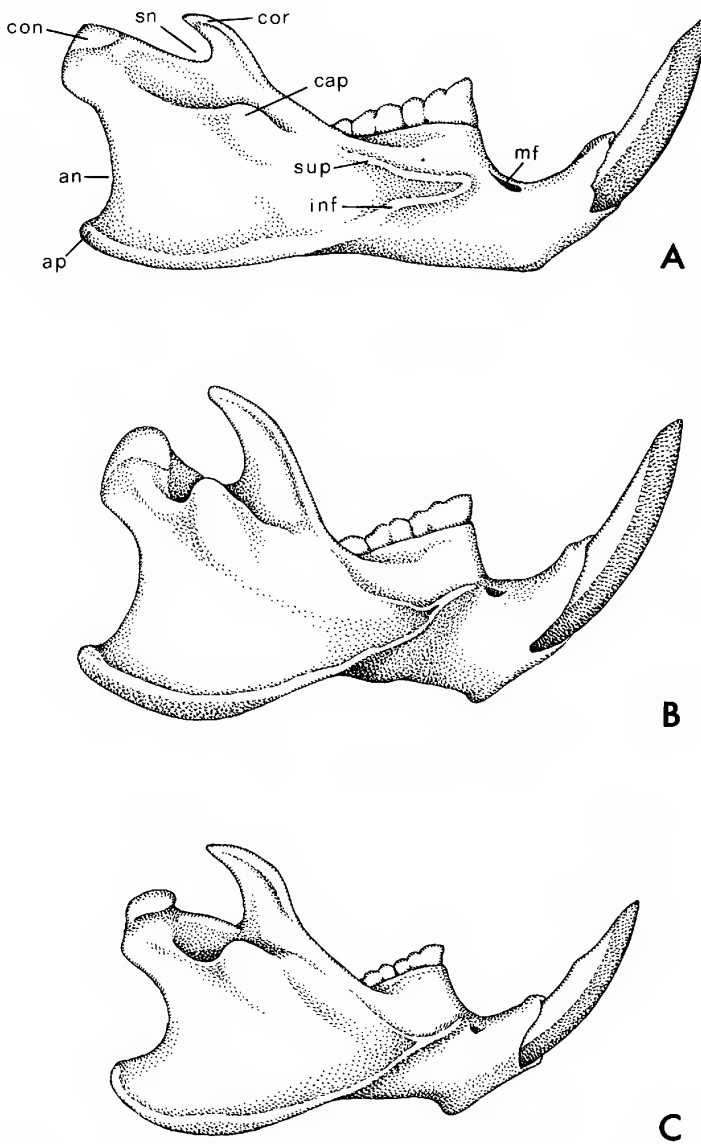


Fig. 11. Lateral views of right mandibles. **A**, *Lundomys molitor* (AMNH 206363); **B**, *Holochilus brasiliensis* (AMNH 206383); **C**, *H. sciureus* (AMNH 210259). Labeled structures include the angular notch (**an**), the angular process (**ap**), the capsular process of the lower incisor alveolus (**cap**), the condylar process (**con**), the coronoid process (**cor**), the inferior masseteric crest (**inf**), the mental foramen (**mf**), the sigmoid notch (**sn**), and the superior masseteric crest (**sup**).

In *Lundomys*, the alveolus of the lower incisor is short and terminates in a small capsular process directly beneath the coronoid process or its leading edge. The lower incisor alveolus of *Holochilus* is substantially longer and terminates in a much larger capsular process below the trailing edge of the coronoid (in some samples of *sciureus*) or below the

sigmoid notch (in *brasiliensis* and other *sciureus*).

The superior and inferior masseteric crests of *Lundomys* converge as a more-or-less open chevron that ends below the middle of m1 or its anterior root. In *Holochilus*, the masseteric crests are closely approximated anteriorly, often forming a single crest that ex-

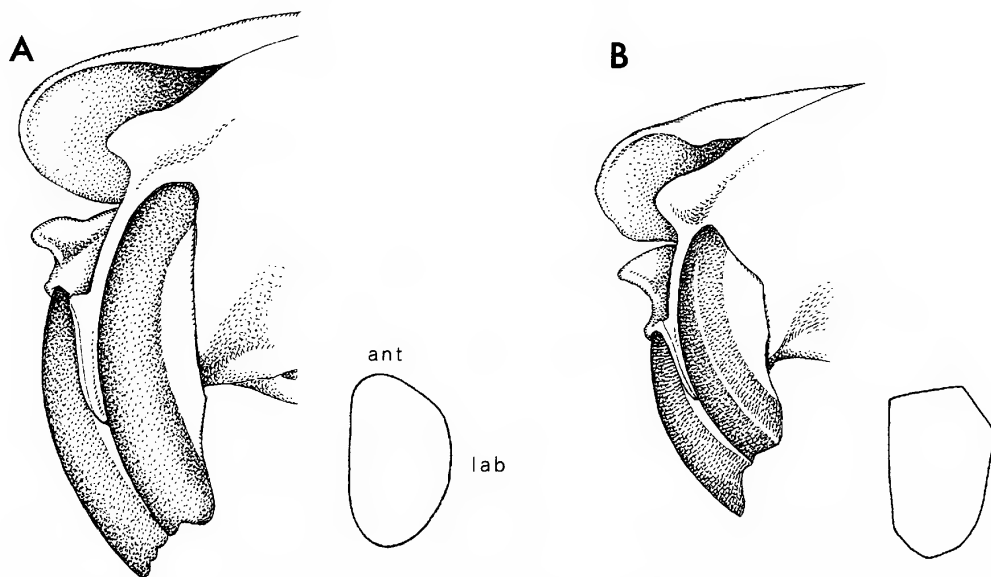


Fig. 12. Oblique views and cross sections of left upper incisors. A, *Lundomys molitor* (AMNH 206368); B, *Holochilus sciureus* (AMNH 210255). ant, anterior; lab labial.

tends beyond the anterior root of m1 and approaches the mental foramen. The degree of conjunction of the masseteric crests is variable within *Holochilus*: consistently long in *H. brasiliensis* and many populations of *H. sciureus*, but shorter in other geographic samples of the latter (whose converging crests resemble the open chevron of *Lundomys* but extend further forward, nearly to the mental foramen).

Collectively, these anatomical differences impart a deeper, stocky appearance to the mandible of *Holochilus* that contrasts with the slender, elongate conformation of this element in *Lundomys*.

DENTITION

Upper incisors: The upper incisors of both *Lundomys* and *Holochilus* are large, strong, opisthodont teeth with yellow-orange enamel bands, but closer inspection reveals consistent differences. The enamel bands that form the anterior surfaces of these teeth are smoothly rounded in *Lundomys* (fig. 12A), whereas the enameled surface of each upper incisor in *Holochilus* is distinctly angular because a flattened medial facet is more-or-less sharply demarcated from a well-defined lateral bevel (fig. 12B).

Molar crown morphology: The molars of both *Lundomys* and *Holochilus* are moderately high-crowned by comparison with those of some pentadelphodont muroids, but the two genera diverge conspicuously in other aspects of their occlusal design. The molars of *Lundomys* retain a bunodont or cuspidate topography, with the principal lingual and labial cusps elevated above a central longitudinal trough; these dental surfaces appear crested in younger specimens, but develop a terraced configuration with wear (descriptive terminology after Hershkovitz, 1955, 1962, 1967). In contrast, the molars of both young and old specimens of *Holochilus* are flat-crowned with cusps and connecting lophs deployed in a single occlusal plane (Hershkovitz, 1955: fig. 142).

In *Lundomys*, the principal cusps are arranged in essentially opposite pairs with their lingual and labial margins bluntly rounded (figs. 5A, 5B, 6A). The principal cusps of *Holochilus sciureus* (figs. 5D, 6C), however, are arranged in an alternating pattern—especially as observed in the relative displacements of the protocone/paracone, hypocone/metacone, and hypoconid/entoconid pairs—and their labial and lingual margins are acutely angled (prismatic). Specimens of *H. brasiliensis* are intermediate to *Lundomys* and *H.*

sciureus with regard to cusp arrangement and prismatic definition.

The labial and lingual folds (flexi/flexids) of *Lundomys* extend only to the midline of the molars and do not interpenetrate. By contrast, certain labial and lingual folds of *Holochilus* extend far beyond the midline, but the pattern of interpenetration differs appreciably between *H. brasiliensis* and *H. sciureus*. The principal lingual fold (hypoflexus) of M1 and M2 is considerably deeper in *H. brasiliensis* than in *H. sciureus*, a difference correlated with the presence of a vestigial mesoloph in the former (see below) and the expanded paracone of the latter.³ Analogous species differences in the lower dentition are also evident.

Mesoloph(id) development provides other important distinctions between *Lundomys* and *Holochilus*. A small but distinct mesoloph (which never reaches the buccal margin) occurs on M1 and M2 but is usually absent from M3 in *Lundomys*; small mesolophids are likewise usually present on m1 and m2 but not on m3. In *Holochilus brasiliensis*, a vestigial mesoloph is sometimes present on M1 and M2, but usually the median mure of those teeth retains only a small deflection that marks the location of the absent structure; in contrast, a well-developed mesoloph is always present on M3. Mesolophids are usually absent in the mandibular dentition of *H. brasiliensis*. No trace of a mesoloph(id) is present on M1, M2, and in the lower dentition of *H. sciureus* (except as rare individual variants), whereas a distinct mesoloph is usually present on M3 (not, however, on the specimen illustrated in fig. 5D). Correlated with the usual presence of a mesoloph on M3 in *Holochilus* species, the length of that tooth is equal to or exceeds the length of M2; in *Lundomys*, the third molar is always smaller than the second.

The two genera contrast in other occlusal features. The anterocone of *Lundomys* is narrow and weakly divided by a shallow anteromedian flexus when unworn, but the broader anterocone of *Holochilus* is undivided. The anteroconid of *Holochilus* is likewise broader than its homolog in *Lundomys*, but in both genera this cusp is undivided and encloses a

deep enameled pit that persists until advanced stages of wear. A small anteroloph is present on the unworn M1 of *Lundomys* but appears to be consistently absent from that tooth in *Holochilus*. A shallow indentation (the protoflexus) consistently demarcates the procingulum from the protocone on the M2 of *Lundomys*; this fold is absent in *Holochilus* and the anteroloph and protocone are therefore merged to form a single broad loph across the front of that tooth.

Molar roots: The upper molars of *Lundomys* each have three large, externally visible roots (anterior, posterior, and lingual); although small accessory rootlets may be present internally, they are invisible when the teeth are still in place (figs. 13A, 13C). In contrast, the first upper molar of *Holochilus* has a prominent fourth root that is clearly visible on the labial side of the tooth (figs. 13B, 13D). In both genera, the first lower molar has two large roots (anterior and posterior) and two accessory rootlets (labial and lingual) that are visible externally in older specimens; m2 and m3 are always two-rooted.

VISCERA

Stomach: The gastric morphology of *Lundomys molitor* closely resembles that illustrated by Carleton and Musser (1989: fig. 28) for *Oryzomys palustris*, and conforms to the unilocular-hemiglandular condition described by Carleton (1973). The gastric lumen is undivided by septa or infolding of the stomach walls, and glandular tissue is restricted to the antrum (right half); the corpus (left half) is entirely lined with cornified epithelium (note that muroid stomachs are conventionally illustrated in ventral view). Some stomachs of *L. molitor* exhibit a slight leftward deflection of the bordering fold from the incisura angularis, but glandular epithelium does not extend beyond the esophagus in any of the specimens we examined (AMNH 206373, 206388, 206392, 206393).

Stomachs of *Holochilus* (Carleton, 1973: fig. 3C) differ consistently from the condition observed in *Lundomys*: the organ is unilocular, but the bordering fold bends abruptly leftward from the incisura angularis and loops far into the corpus before curving back again

³ Species differences first noted by Massoia (1981).

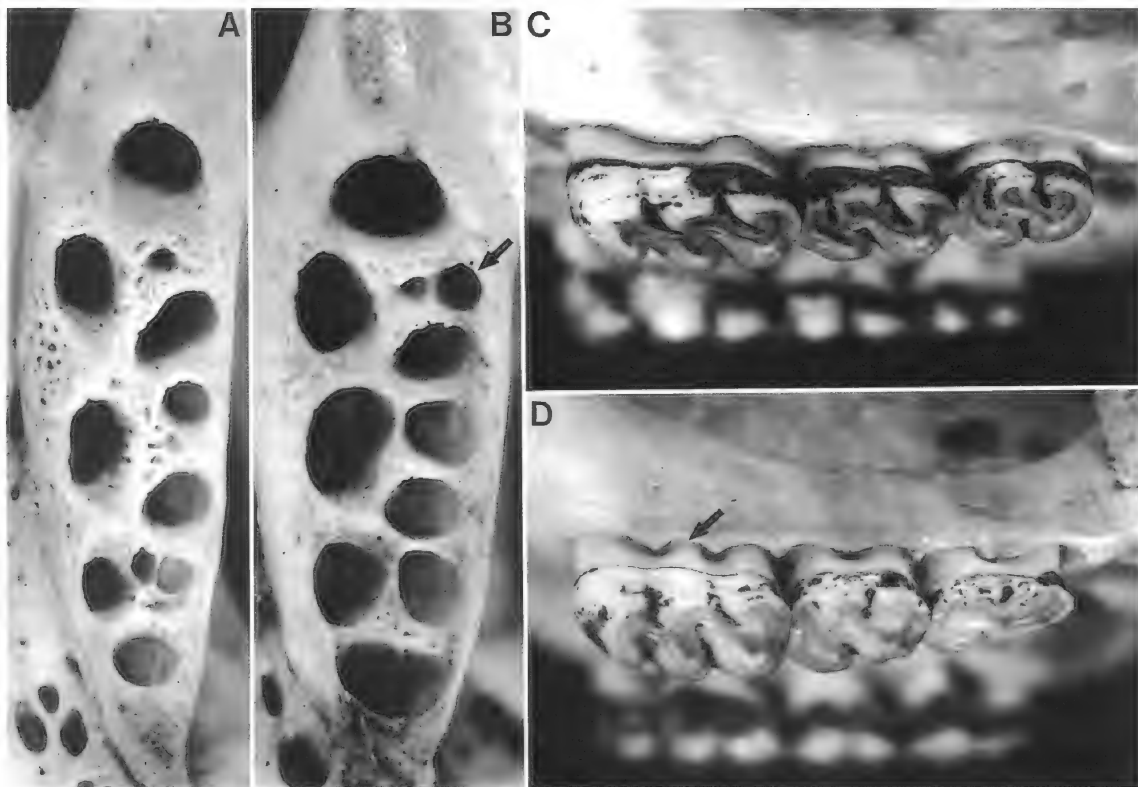


Fig. 13. Upper molar alveoli and molar roots of *Lundomys molitor* and *Holochilus brasiliensis*. A, left upper molar alveoli of *L. molitor* (AMNH 286380); B, the same of *H. brasiliensis* (AMNH 206378); C, labial view of left upper molars of *L. molitor* (AMNH 206393); D, the same of *H. brasiliensis* (AMNH 206362). The arrow in B indicates the alveolus of the labial molar root of M1 in *H. brasiliensis*; the arrow in D indicates the root itself, which is exposed in older specimens. Both structures are absent in *L. molitor*.

to cross the greater curvature at a point about opposite the esophagus. This morphology occurs without appreciable differences in specimens of *H. brasiliensis* from Argentina (MSU 17892, 18692, 18797, 19355) and of *H. sciureus* from Bolivia (AMNH 210286), Paraguay (UMMZ 124225, 124226, 125484, 133970), and Venezuela (AMNH 257335, 257336, 266925).

Gall bladder: The absence of gall bladders in *Lundomys* and *Holochilus* was reported by Voss (1991: table 4, Appendix 2) from dissections of two specimens of *L. molitor* (identified as *H. magnus* therein) and two of *H. "brasiliensis"* (sensu Hershkovitz, 1955); the latter (AMNH 257335 and 257336, from Venezuela) are referable to *H. sciureus* in the sense of this report. We have since confirmed the absence of gall bladders in *H. brasiliensis* (sensu stricto: MSU 17892, 18692, 18797)

and in additional examples of *H. sciureus* from Paraguay (UMMZ 124225, 124226, 125484, 133970) and Bolivia (AMNH 210286).

PHYLOGENETIC RELATIONSHIPS

Current knowledge of higher-order relationships among muroid rodents provides an insecure foundation for phylogenetic studies at lower taxonomic levels. Ideally, we would like to accept a well-corroborated hypothesis of monophyly for some group that includes *Lundomys*, *Holochilus*, and other Neotropical genera, and identify outgroups in order to polarize the character transformations of interest. Unfortunately, compelling evidence of monophyly for the subfamily Sigmodontinae (sensu Carleton and Musser, 1984) is lacking and the current tribal-level classifi-

TABLE 4
Outgroup Exemplars Surveyed
 (See accompanying text for explanation)

Tylomyines^a

Nyctomys sumichrasti
Otonyctomys hatti
Otitylomys phyllotis
Tylomys mirae

Neotomines^a

Hodomys alleni
Nelsonia neotomodon
Neotoma (N.) floridana
Neotoma (Teanopus) phenax
Neotoma (Teonoma) cinerea
Xenomys nelsoni

Peromyscines^b

Habromys lepturus
Isthmomyss pirrensis
Megadontomys thomasi
Neotomodon alstoni
Onychomys leucogaster
Osgoodomys banderanus
Peromyscus leucopus
Podomys floridanus

Incertae sedis

Baiomys musculus
Ochrotomys nuttalli
Reithrodontomys (Aporodon) creper
Reithrodontomys (R.) sumichrasti
Scotinomys xerampelinus

^a After Carleton (1980).

^b After Carleton (1989).

cation of South American muroids (e.g., as summarized by Reig, 1984: table 16-1) is thoroughly unsatisfactory from a phylogenetic perspective (see Carleton and Musser, 1989: 53–55; and Voss, 1991: 33–37). Nevertheless, some provisional hypothesis of monophyly must be adopted for any progress to be made in understanding the phylogenetic significance of character distributions in the Neotropical fauna.

For the purpose of the analyses that follow, we assume the monophyly of a predominantly Neotropical group of sigmodontine genera in which (1) the entepicondylar foramen of the humerus is absent, (2) the entoglossal process of the basihyal is absent, (3) the tuberculum of the first rib articulates with the transverse processes of the seventh cervical and first thoracic vertebrae, and (4) the glans penis is complex (see Carleton, 1980,

for discussions of the polarity of these character states, and Voss, 1988: 437, for comments about their distribution among Neotropical muroids). This group apparently coincides with the “South American Crice-tines” of Hooper and Musser (1964) minus *Nyctomys* (a Central American tylomyine), and with Reig’s (1980) concept of Sigmodontinae.

In order to polarize character transformations in the Neotropical muroid fauna, we assume that reasonable outgroup comparisons can be made to North and Central American tylomyines, neotomines, peromyscines, and other genera with simple phalli (Carleton, 1980, 1989). As noted by Voss (1993), this assumption is supported principally by geographic propinquity and biochemical results because morphological evidence that these northern taxa are closely related to Neotropical muroids is currently unavailable. Carleton (1980: table 7) provided much useful outgroup data for the present study, but we examined outgroup exemplars (table 4) for new and hitherto unpolarized characters.

We focus on two rival hypotheses about the relationships of *Holochilus* (sensu lato). Derived resemblances in craniodental morphology noted by Wagner (1842), Winge (1887, 1941), Thomas (1928), Ellerman (1941), and Hershkovitz (1955) suggest that *Holochilus* and *Sigmodon* are closely related, an hypothesis that appeared compelling to Reig (1984) whose tribe Sigmodontini contained only these two genera. Hooper and Musser (1964), however, reported similarities in phallic characters between *Holochilus* and certain species of *Oryzomys* and suggested that the former might be an oryzomyine rather than a member of Hershkovitz’s (1955) sigmodont group. Additional evidence that *Holochilus* and oryzomyines (sensu Hershkovitz, 1944, 1960) may be closely related was discussed by Baker et al. (1983) and Voss (1991).

The taxonomic units of our analysis include *Sigmodon hispidus*, *S. peruanus*, *Lundomys molitor*, *Holochilus brasiliensis*, *H. sciureus*, *Oryzomys subflavus*, and *Pseudoryzomys simplex*. The two species of *Sigmodon* were chosen to represent substantially divergent morphologies within the genus; ex-

TABLE 5
Morphological Characters of Seven Neotropical Muroids and a Hypothetical Ancestor

	Characters ^a																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Ancestor	a	a	a	a	a	a	a	a	?	a	a	a	a	a	a	a	a	a	a	?	a	a	a	a	a
<i>Holochilus brasiliensis</i>	b	b	b	c	a	b	b	b	a	a	b	b	b	b	b	b	a	c	b	b	c	b	b	b	b
<i>Holochilus sciureus</i>	b	b	b	c	a/b	b	b	b	a	a	b	b	b	b	c	c	a	c	b	b	c	b	b	b	b
<i>Lundomys molitor</i>	b	b	b	c	a	b	a	a	b	b	b	b	a	a	a	b	b	b	a	b	b	a	b	a	b
<i>Oryzomys subflavus</i>	a	a	a	a	a	a	b	a	b	b	b	b	a	a	a	a	a	a	a	b	a	b	b	a	b
<i>Pseudoryzomys simplex</i>	a	a	b	b	a	b	b	a	b	b	b	b	a	a	a	b	b	c	a	b	c	b	b	b	b
<i>Sigmodon hispidus</i>	a	a	a	a	b	b	b	a	b	a	b	a	a	b	a	b	c	b	c	b	a	c	b	b	a
<i>Sigmodon peruanus</i>	a	a	a	a	b	b	b	a	a	a	a	a	a	b	c	c	b	c	b	a	c	b	a	?	?

^a Numbered and described in the text.

cept as noted below, character information for both was extracted from Voss (1992). *Holochilus brasiliensis* and *H. sciureus* are included separately to test generic monophyly and to distinguish interspecific character differences from character variation of unknown significance within the latter taxon. *Oryzomys subflavus*⁴ is a South American congener of the North American type species (*O. palustris*) which it closely resembles in many characters; our character data for this taxon were obtained from Bolivian and Paraguayan series in the AMNH and UMMZ collections. *Pseudoryzomys* is an enigmatic, monotypic South American genus that may be closely related to oryzomyines (Voss and Myers, 1991; Voss, 1991); in the course of preparing this report, we observed many striking similarities between *Pseudoryzomys* and *Lundomys* that clearly merit evaluation in a phylogenetic context. Except as noted below, character information for *P. simplex* was extracted from Voss and Myers (1991). Many characters are known to vary among these seven taxa, but not all are useful for analyzing phylogenetic relationships. We ex-

cluded autapomorphies and uninformative characters (e.g., unordered multistate characters with only a single state expressed by more than one taxon). Some characters that afford clear distinctions between *Lundomys* and *Holochilus* (e.g., size of the ectotympanic bullae, relative size of the pregenoid foramen and subsquamosal fenestra, mandibular morphology) proved intractable when we tried to define states for other taxa, and these were also omitted from our analysis. Where we recorded only the modal character state, this fact is noted in the character-state description (e.g., “usually present”) or we describe the variation explicitly in the remarks that follow. Multistate morphological characters are ordered as specified in the state descriptions. Our final data set (table 5) includes a hypothetical ancestor, reconstructed by outgroup analysis, as the designated root for our trees.

We analyzed phylogenetic relationships using the exhaustive search option of PAUP Version 3.1 (Swofford, 1993) to find trees of minimal length by the criterion of unweighted Wagner parsimony (forward and reversed transformations of all characters counted equally). Descriptive statistics for trees (length, L; and consistency index, CI) were defined by Kluge and Farris (1969). Our tree diagrams were drawn by MacClade (Maddison and Maddison, 1992).

CHARACTER DEFINITIONS

1. Ungual tufts on hindfoot: (a) present; (b) absent.

Remarks.—As noted by Voss (1993), tufts

⁴ We provisionally use *Oryzomys subflavus* (Wagner) for Brazilian, Paraguayan, and Bolivian populations with the anatomical traits described and tabulated herein. We follow Cabrera (1961) by regarding *Mus vulpinus* Lund and *Calomys laticeps* Winge as synonyms. *Oryzomys buccinatus* (Olfers), based on Azara's (1801) ambiguous description of the “*Rat troisième ou rat angouya*,” is sometimes used in reference to Bolivian and Paraguayan specimens (Musser and Carleton, 1993). The convoluted taxonomy of this morphologically distinctive species will be discussed elsewhere (R. S. Voss and P. Myers, in prep.).

of long ungual hairs are uniformly present in tylomyines, neotomines, peromyscines, and other North and Central American outgroups. Voss (1992) described the manus and pes of *Sigmodon* as "without conspicuous tufts of longer hairs at the bases of claws," but that description was intended to distinguish the long but sparse ungual hairs of *Sigmodon* from the thick and very obvious tufts present in certain other Neotropical muroids; the claws of *Sigmodon* are not naked like those of *Lundomys* and *Holochilus*. Ungual tufts are coded as "present" if the hairs rooted at the bases of the claws equal or exceed the claws in length, and as "absent" if the hairs are always much shorter than the claws.

2. Natatory fringe on hindfoot: (a) absent; (b) present.

Remarks.—Natatory fringes are not present in any outgroup taxa. The highly developed natatory fringes of *Lundomys* are autapomorphic and simple presence is therefore coded for both that genus and *Holochilus*.

3. Plantar pads on hindfoot: (a) thenar, hypothenar, and four interdigital pads present and well developed; (b) all pads very small, hypothenar usually absent.

Remarks.—All tylomyines, neotomines, and most peromyscines have six well-developed plantar pads. Among the outgroups, only *Onychomys* and *Podomys* (both peromyscines) lack one or both of the metatarsal pads, losses that Carleton (1980) interpreted as autapomorphies as we do also. The hypothenar of *Oryzomys subflavus* is very small but appears to be present in all of the specimens at hand.

4. Interdigital webbing on hindfoot: (a) absent; (b) present but small, not extending to first interphalangeal joint of any digits; (c) present, extending to or beyond first interphalangeal joints of digits II, III, and IV (derived from state b).

Remarks.—Interdigital webbing is another trait that is not developed in any of the North and Central American outgroups. The ordering of the states recognized above is linear, following our perception of a graded series of successively more derived morphologies among the taxa of our study. Although Hershkovitz (1944: 12) claimed that the three middle digits of the hindfoot are "partly, but not always conspicuously webbed" in all ory-

zomyines, we observed no interdigital webbing on the hindfeet of *Oryzomys subflavus*.⁵ The highly developed webs of *Lundomys* are autapomorphic and therefore are not distinguished from the less extensive webs of *Holochilus* in our character-state coding.

5. Mammary counts: (a) eight (thoracic teats absent); (b) ten (thoracic teats present).

Remarks.—All tylomyines, neotomines, peromyscines, and other North and Central American outgroup taxa have either four or six teats in inguinal, abdominal, and (in taxa with six) postaxial pairs (Carleton, 1980; but note that an alternative nomenclature for mammary loci is used therein). Derived mammary counts of eight or more in many Neotropical muroids always include a pectoral pair (Voss, 1988), and counts of ten include thoracic teats as well. We coded mammary variation within the *H. sciureus* complex as taxonomic (rather than population) polymorphism because it apparently occurs only among geographic samples (table 3) that may prove to represent distinct species.

6. Anterodorsal margin of zygomatic plate: (a) smoothly rounded, without a sharp corner or spinous process; (b) produced as a sharp corner or spinous process.

Remarks.—A sharp anterior corner or spinous process extending the free dorsal margin of the zygomatic plate is absent in all outgroup taxa, many of which lack well-defined zygomatic notches (Carleton, 1980).

7. Supraorbital margins: (a) without raised beads; (b) with raised beads, at least in older specimens.

Remarks.—Beaded and unbeaded supraorbital margins both occur among the outgroups, but we concur with Hershkovitz (1962) and Carleton (1980) that the beadless morphology is plesiomorphic. The supraorbital margins are unambiguously beaded or not in most of the taxa included in our analysis, but many specimens of *Pseudoryzomys simplex* have indistinct supraorbital beads.

8. Postorbital ridge: (a) absent, posterior

⁵ The bases of the digits are, of course, connected by the integument, so pulling adjacent toes in opposite directions will always raise a small bridge of skin between them. Interdigital webs are to be distinguished from such anatomically trivial effects.

orbital wall without conspicuous relief, frontal-squamosal suture exposed; (b) present and concealing frontal-squamosal suture in most older specimens.

Remarks.—A thick postorbital ridge that obscures the frontal-squamosal suture is uniformly absent among the outgroup taxa we surveyed.

9. Incisive foramina: (a) short, not extending posteriorly to or between molar alveoli except in juveniles and some young adult specimens; (b) long, extending to or between molar alveoli in all or most adult specimens.

Remarks.—Long and short incisive foramina are both represented among the outgroup exemplars we surveyed (table 4) with no compelling taxonomic pattern to suggest which is primitive for Neotropical muroids. We therefore coded the ancestral state for this character as unknown.

10. Alisphenoid strut: (a) present, buccinator-masticatory and accessory oval foramina separate; (b) absent, buccinator-masticatory and foramen ovale confluent.

Remarks.—An alisphenoid strut separates the buccinator-masticatory and accessory oval foramina in all of the outgroup samples examined by Carleton (1980),⁶ and we therefore interpret the strut as primitively present among Neotropical muroids. The alisphenoid strut was reported as present or absent in *Pseudoryzomys simplex* by Voss and Myers (1991), but it is usually absent (in ten specimens with undamaged alisphenoids, the strut is completely absent in six, present unilaterally in three, and present on both sides in only one).

11. Carotid circulation: (a) with complete stapedia contribution to the facial (internal maxillary and ophthalmic) supply; (b) without any stapedia contribution to the facial supply.

Remarks.—We follow the now-standard phylogenetic interpretation of muroid carotid arterial variation (Bugge, 1970; Carleton, 1980; Voss, 1988; Carleton and Musser, 1989)

⁶ Absence of an alisphenoid strut in the sense of this report is equivalent to absence of a foramen ovale in Carleton (1980). In the course of checking outgroup exemplars (table 4), however, we noted some polymorphism for this character within and among samples of *Onychomys leucogaster*.

by regarding a complete stapedia contribution as primitive. Intermediate states for this character are not exhibited by any of the taxa included in our analysis.

12. Bullar suspension: (a) posterior suspensory process of squamosal present and connected to the tegmen tympani; (b) posterior suspensory process absent, tegmen tympani not touching or barely in contact with squamosal.

Remarks.—The polarity of this character was discussed by Voss (1993) who reported that in all outgroup taxa the tegmen tympani is tightly connected to the squamosal. Our character-state coding emphasizes presence or absence of the posterior suspensory process, not contact between the tegmen tympani and the squamosal per se.

13. Enamel band of upper incisors: (a) smoothly rounded or flattened, but without labial bevel; (b) flattened medially, with distinct labial bevel.

Remarks.—Although a few outgroup taxa have flattened enamel bands (e.g., *Onychomys* species), none exhibits the prominent labial bevel characteristic of *Holochilus* species.

14. Molar occlusal topography: (a) bunodont; (b) flat-crowned.

Remarks.—Among the outgroups, only neotomines and *Neotomodon alstoni* (a peromyscine) have flat-crowned molars. Hinton (1926), Hershkovitz (1967), Vorontsov (1979), and Carleton (1980) are among the many students of muroid dental morphology who have interpreted bunodont dentitions as plesiomorphic, and we see no reason to contradict this broad consensus in the present analysis.

15. Molar occlusal design: (a) cusps essentially opposite with rounded outer margins (not prismatic), lingual and labial folds not interpenetrating; (b) cusps slightly alternating with more acute outer margins, some lingual and labial folds deeply interpenetrating; (c) cusps conspicuously alternating with acute outer margins (prismatic), some lingual and labial folds deeply interpenetrating (derived from state b).

Remarks.—Our description of states for this character reflects the obvious interrelationship of cusp position, cusp shape, and fold morphology in molar occlusal pattern

definition. Our scoring of taxa emphasizes the upper dentition, in which differences are most apparent. Carleton (1980) and Voss (1993) provided our rationale for supposing that the ancestral Neotropical muroid molar had opposite, rounded cusps and folds that did not interpenetrate.

16. Mesoloph on M1 and M2: (a) mesoloph large, extending from median mure to labial cingulum (fused with mesostyle); (b) mesoloph small, not or seldom extending to labial cingulum (not fused with mesostyle), sometimes absent from worn teeth, or reduced to a slight but perceptible labial deflection of median mure; (c) mesoloph absent (derived from state b).

Remarks.—Although mesoloph(id)s are present or absent in various outgroup taxa, we follow the orthodox interpretation (e.g., Stehlin and Schaub, 1951; Hershkovitz, 1962, 1967; Carleton, 1980) of muroid dental evolution by assuming that pentalophodont molars (with well-developed accessory crests) are primitive.

17. Mesoloph on M3: (a) usually present and well developed; (b) absent or vestigial.

Remarks.—Our ancestral character-state assignment for this character follows the prevailing consensus (see the analysis for character 16). The taxonomic distribution of the mesoloph on M3 vs. M1–2 (table 4) clearly indicates that this serially homologous crest has undergone independent evolutionary transformations on different teeth.

18. Anteroloph on M1: (a) present and well developed, extending to labial cingulum; (b) small, not extending to cingulum; (c) absent (derived from state b).

Remarks.—A well-developed anteroloph is part of the plesiomorphic, pentalophodont bauplan (see the analysis for character 16).

19. Protoflexus of M2: (a) present as a shallow indentation, at least in unworn dentitions; (b) absent.

Remarks.—The protoflexus separates the procingulum from the protocone in primitive, pentalophodont dentitions (see Reig, 1977: fig. 3).

20. Internal enameled pit of m1 procingulum: (a) absent; (b) present.

Remarks.—None of the outgroup exemplars that we examined (table 4) have a large enameled pit in the procingulum of m1. In

many outgroup taxa with divided anteroconids, however, the internal sulcus of the anteromedian flexid is deeper than the crevice that communicates with the anterior margin of the tooth and is often isolated by wear as a small enamel island. The large pit in the m1 procingulum of *Holochilus*, *Lundomys*, *Oryzomys subflavus*, and *Pseudoryzomys* may be a phylogenetic remnant of an ancestral anteromedian flexid; certainly, it appears to be a derived trait. The undivided, unpitted anteroconid of *Sigmodon* may be ancestral to the divided morphology (Carleton, 1980: character 2), or may have evolved from the pitted condition by loss of the pit. We regard the ancestral state for this character as unknown.

21. Mesolophids in lower dentition: (a) present and well developed, extending to lingual cingulum; (b) present in unworn dentitions but small, not extending to lingual cingulum; (c) absent (derived from state b).

Remarks.—We follow the standard interpretation of muroid molar evolution for this character (see analysis for character 16).

22. Labial root of M1: (a) absent; (b) present.

Remarks.—An externally visible labial root is absent from M1 in all of our outgroup exemplars. Carleton (1980: table 7) recorded an internal “labial” root for *Reithrodontomys sumichrasti* and *Megadontomys thomasi* (outgroup species that we also examined: table 4), but as internal roots and labial roots sometimes occur on the same tooth (fig. 13B) they should be distinguished in phylogenetic analyses. Externally visible labial roots are present in *Reithrodontomys megalotis* and *R. montanus* (Carleton, 1980: table 7), but the plesiomorphic state for Neotropical muroids is probably absence.

23. Accessory roots of m1: (a) only labial accessory root usually present (three roots total); (b) labial and lingual accessory roots usually present (four roots total).

Remarks.—Lingual rootlets appear to be uniformly absent from the first lower molars of tyromyines, neotomines, peromyscines, and other North and Central American outgroup taxa (Carleton, 1980).

24. Gastric glandular epithelium: (a) restricted to antrum (stomach strictly hemi-

glandular); (b) extends beyond esophagus, into corpus.

Remarks.—Although both of the states that we recognize for this character were subsumed in the unilocular-hemiglandular morphotype that Carleton (1973, 1980) hypothesized to be primitive for muroids, the pronounced leftward extension of glandular tissue into the corpus of *Holochilus* and *Sigmodon hispidus* (both described in Carleton, 1973) differs conspicuously from the strictly hemiglandular condition defined herein. Because several outgroup taxa have strictly hemiglandular stomachs (species of *Tylomys*, *Ototylomys*, *Scotinomys*, and *Baiomys*; Carleton, 1973) whereas none have glandular epithelium in the corpus, we assume that the former condition is primitive for Neotropical muroids. The two available stomachs of *Pseudoryzomys simplex* (UMMZ 133912, 134387) were originally described by Voss and Myers (1991) as hemiglandular (sensu Carleton, 1973, 1980) but each has a well-defined extension of glandular epithelium into the corpus. The gastric morphology of *Sigmodon peruanus* is unknown.

25. Gall bladder: (a) present; (b) absent.

Remarks.—We follow Vorontsov (1979), Carleton (1980), and Voss (1991) in assuming that absence of the gall bladder is derived. Although Voss (1992) included presence of a gall bladder in his diagnosis of *Sigmodon*, this character state has yet to be confirmed for *S. peruanus* because fluid-preserved specimens are not available.

RESULTS

The shortest tree for our character data (fig. 14A) supports Hershkovitz's (1955: 653) suggestion that "... *Sigmodon* is most nearly related to *Holochilus* and, in most respects, nearer *H. brasiliensis* than the latter is to its larger congener *H. magnus*," but the illustrated cladistic position of *Pseudoryzomys* was not predicted by any prior systematic study of Neotropical muroids. This topology is primarily determined by a set of mutually compatible dental characters and illustrates a sequence of taxa with molars progressively simplified and transformed from the bunodont, pentalophodont morphology of *Ory-*

zomys to the planar, tetralophodont configuration of *Sigmodon* and *Holochilus*.

The monophyletic group that includes *Lundomys*, *Pseudoryzomys*, *Sigmodon*, and *Holochilus* in this phylogenetic reconstruction (fig. 14A) is supported by four unique and unreversed character transformations (apomorphic states in parentheses): acquisition of a sharp anterodorsal corner or spinous process on the zygomatic plate (6b), reduction of mesolophids on M1–2 (16b), reduction of the anteroloph of M1 (18b), and reduction of mesolophids (21b). The next node from the root is diagnosed by three uniquely derived and unreversed transformations that *Pseudoryzomys* shares with *Sigmodon* and *Holochilus*: loss of the anteroloph of M1 (18c), loss of mesolophids (21c), and extension of glandular epithelium into the gastric corpus (24b). Finally, a sister-group relationship between *Sigmodon* and *Holochilus* is supported by three uniquely shared and unreversed character states: flat-crowned molars (14b), the alternating arrangement of molar cusps separated by interpenetrating folds (15b), and absence of the protoflexus of M2 (19b). The two species of *Holochilus* uniquely share derived states of posterior orbital morphology (8b) and incisor shape (13b). No unique apomorphies are shared by the two species of *Sigmodon*, whose close relationship is instead supported by homoplastic character transformations.

The next-most-parsimonious phylogeny (fig. 14B) depicts alternative groupings determined by a set of mutually compatible external characters: *Pseudoryzomys* uniquely shares derived transformations of plantar pads (3b) and interdigital webs (4b) with *Lundomys* and *Holochilus*; and *Lundomys* and *Holochilus* share uniquely transformed ungual tufts (1b), natatory fringes (2b), and interdigital webs (4c). Obviously, many of the dental traits interpreted as synapomorphies of monophyletic groups in figure 14A are less parsimoniously explained in this reconstruction as independently derived traits of *Sigmodon*, *Pseudoryzomys*, and *Holochilus*.

Phylogenetic hypotheses that recognize *Holochilus*, *Lundomys*, and *Pseudoryzomys* as oryzomyines (i.e., as members of a monophyletic group that includes *Oryzomys* but not *Sigmodon*) are much less parsimonious

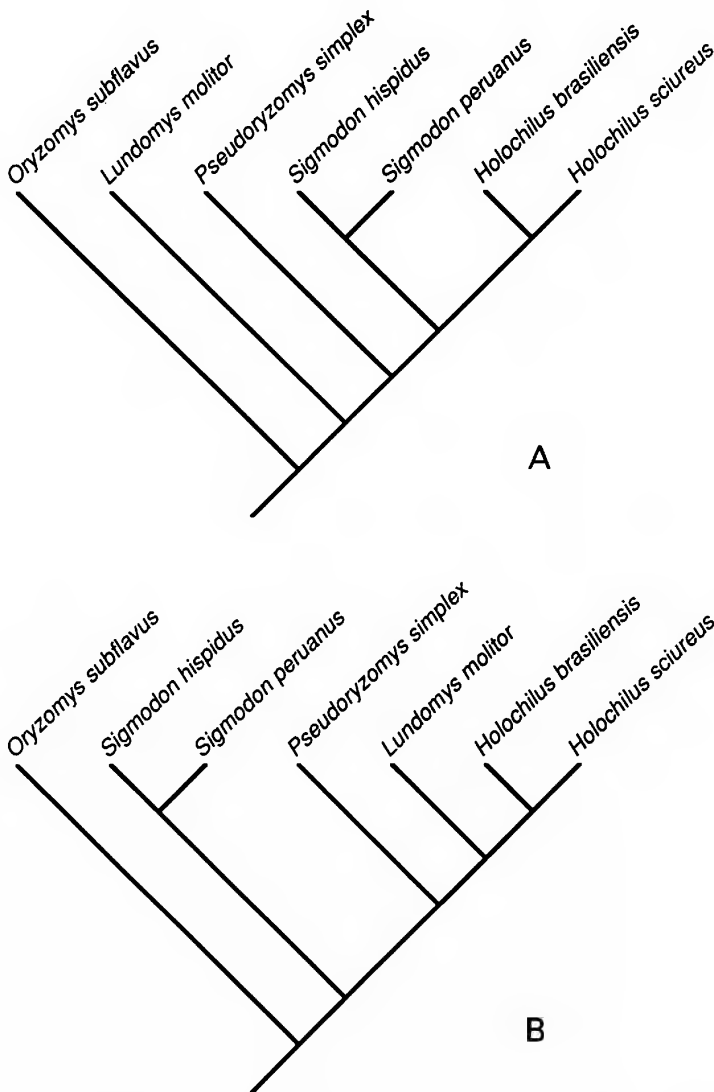


Fig. 14. Two hypotheses of phylogeny for our character data (table 5). A, the most-parsimonious tree (L = 46, CI = 0.65); B, the next-most-parsimonious alternative (L = 48, CI = 0.62).

than the preceding examples (fig. 15). Nevertheless, such trees are supported by three uniquely derived and unreversed attributes: absence of a posterior suspensory process of the squamosal (12b), a large enamel pit in the procingulum of m1 (20b), and absence of a gall bladder (25b). If these derived traits are homologous, then the numerous apomorphic dental resemblances between *Sigmodon* and *Holochilus* are perforce convergent. Although parsimony clearly favors the hypothesis that *Holochilus* and *Sigmodon* are sister taxa, it is noteworthy that almost half

of the characters in our data represent dental comparisons. Including so many characters from a single anatomical system has the obvious risk that convergent adaptations rather than shared ancestry could determine the topology of phylogenetic reconstructions. *Sigmodon* and *Holochilus* are both herbivores that principally subsist on the green, vegetative tissues of grasses and forbs (references cited in Voss, 1992). The flat-crowned, lophodont molar architecture that constitutes the principal evidence of close relationship between these genera conforms to the general

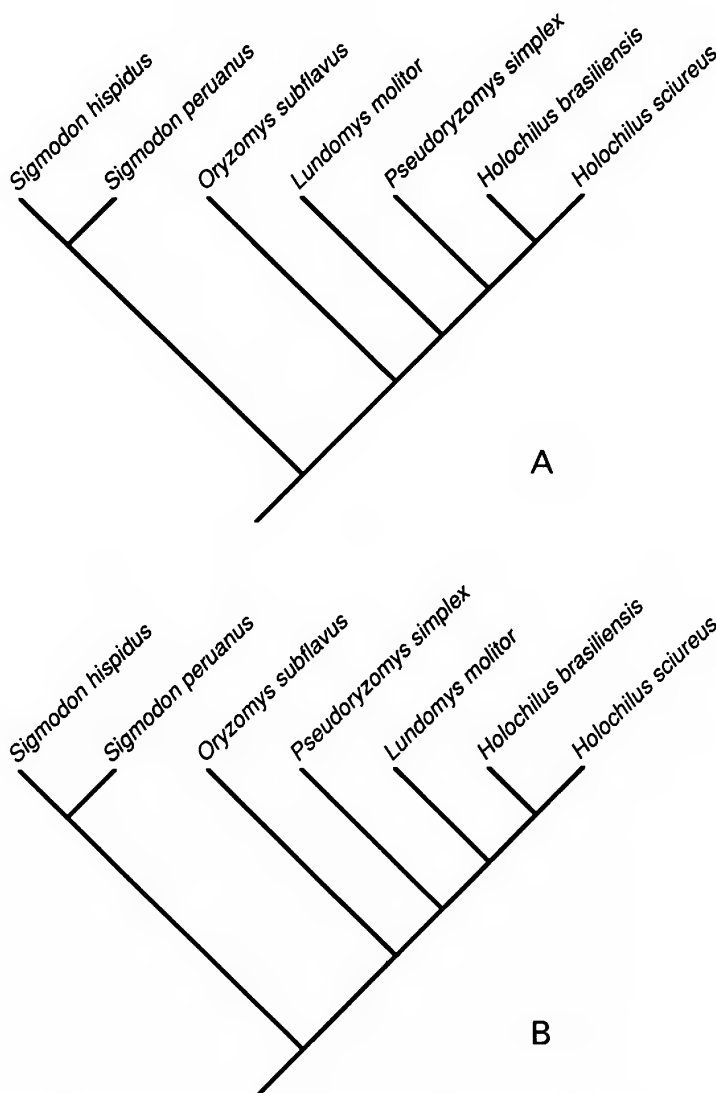


Fig. 15. The two most parsimonious phylogenies for our character data (table 5) under the constraint that *Holochilus*, *Lundomys*, and *Pseudoryzomys* are oryzomyines. The statistics for both trees are identical ($L = 53$, $CI = 0.57$).

occlusal design common to many mammals that eat plant vegetative tissues (Rensberger, 1973; Janis and Fortelius, 1988), so an ad hoc hypothesis of functional convergence is not implausible.

Evidence that *Holochilus* is more closely related to oryzomyines than to *Sigmodon* has been cited in surveys of genitalic and chromosomal characters. Hooper and Musser (1964) reported detailed similarities between the glandes penes of *Holochilus* and *Oryzomys*, and emphasized that the phallic characters of *Sigmodon* (described by Hooper,

1962) are strikingly divergent. Unfortunately, primitive and derived character states of the glans penis were not distinguished, and no tabular summary of character data was provided for analysis. Hooper and Musser's (1964: 45) cautious suggestion that "the position of *Holochilus* be reexamined with the thought in mind that it may be a well differentiated oryzomyine rather than a sigmodont" provoked Hershkovitz (1966: 130) to argue that "a combination of fundamental cranial, dental, and external characters . . . unite *Sigmodon*, *Reithrodon*, *Neotomys*, and

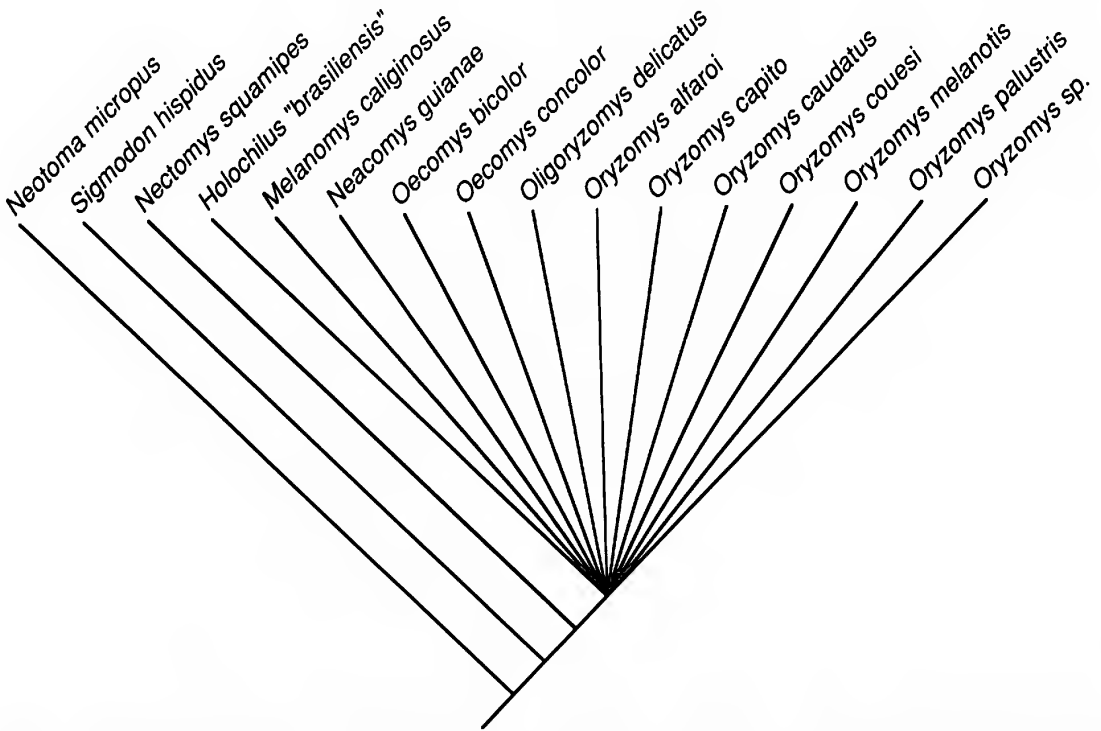


Fig. 16. The strict consensus of 10,000 equally parsimonious phylogenies (each with $L = 46$ and $CI = 0.98$) for 16 muroid species with G-banded karyotypes. The data of Baker et al. (1983) were reanalyzed as unordered characters, and trees were rooted with *Neotoma micropus* as the designated outgroup (see Appendix). The generic taxonomy has been updated to reflect current usage (Musser and Carleton, 1993) but specific epithets follow Baker et al.'s (1983) identifications.

Holochilus into a closely knit group," yet only their "sigmodont" molar morphology uniquely distinguishes these genera as a group apart from other Neotropical muroids. Subsequent suggestions that *Neotomys* and *Reithrodon* are phyllotines (Pearson and Patton, 1976; Olds and Anderson, 1989; Braun, 1993) imply that sigmodont dentitions have arisen at least twice in Neotropical muroid evolution.

Comparisons of G-banded chromosomes among *Holochilus*, *Sigmodon*, and 13 species of oryzomyines were interpreted by Baker et al. (1983) as corroborating Hooper and Musser's (1964) hypothesis that *Holochilus* might be an oryzomyine. We agree. Although our reanalysis (see Appendix) produced a much less resolved phylogeny (fig. 16) than that originally proposed by Baker et al. (1983: fig. 4), their conclusion that *Holochilus* belongs in a monophyletic group with *Nectomys squamipes* and other oryzomyines, but ex-

cluding *Sigmodon*, is unambiguously supported by the karyotypic data they published.

Voss (1991) suggested that absence of a gall bladder supports the monophyly of a group comprising *Holochilus* (sensu lato), *Pseudoryzomys*, *Zygodontomys*, and the oryzomyine genera of Hershkovitz (1944, 1960). The present report summarizes additional evidence that we believe justifies formal recognition of the tribe Oryzomyini with essentially the same membership (see below). Although this taxonomic action is not consistent with the most parsimonious interpretation of our own data, the phylogenetic congruence of certain cranial and visceral characters with the results of prior genitalic and karyotypic studies appears persuasive despite our inability to include the total evidence in a single analysis.

Within the Oryzomyini, *Lundomys* appears most closely related to *Holochilus* and *Pseudoryzomys*, but two different hypotheses

of phylogeny for these genera provide equally parsimonious explanations of our character data. A sister-group relationship between *Holochilus* and *Pseudoryzomys* (fig. 15A) is supported by apomorphic states of dental and gastric characters (18c, 21c, 24b), whereas external apomorphies (1b, 2b, 4c) suggest that *Lundomys* and *Holochilus* are more closely related (fig. 15B). Although we are impressed by the close overall resemblance in size and external appearance between *Lundomys molitor* and *Holochilus brasiliensis*, we acknowledge the genuine ambiguity of the character data analyzed herein and decline to advocate either of these phylogenetic alternatives. Chromosomal, molecular, and genitalic characters will perhaps prove useful in future efforts to resolve this trichotomy.

PHYLOGENETIC DIAGNOSIS AND CONTENTS OF ORYZOMYINI

As explained by Carleton and Musser (1989) and Voss (1991, 1993), the concept of an oryzomyine group emerged gradually in the taxonomic literature on Neotropical muroids. Common to all concepts of this group, as explicitly stated in diagnoses (e.g., Thomas, 1917; and Hershkovitz, 1944, 1960) or implied by lists of included genera (e.g., Tate, 1932; Reig, 1984, 1986), is the shared possession of pentalophodont molars with well-developed mesoloph and mesolophids. Thus, whether oryzomyines were construed narrowly (as by Hershkovitz, 1944, 1960) or in a broader sense (Vorontsov, 1959; Reig, 1980, 1984, 1986), the group was perceived in contradistinction to tetralophodont genera (e.g., akodonts, phyllotines, and sigmodonts) that lack well-developed mesoloph and mesolophids. Unfortunately, pentalophodonty is a primitive trait for muroids (Stehlin and Schaub, 1951; Hershkovitz, 1962, 1967; Reig, 1977), so the traditional "evidence" for group recognition is based on symplesiomorphy (Voss, 1991).

Our concept of Oryzomyini differs from the aforementioned classifications by including several tetralophodont genera: *Holochilus*, *Lundomys*, *Pseudoryzomys*, and *Zygodontomys*. Justification for this revision of tribal contents is summarized in the phylogenetic diagnosis given below. A phyloge-

netic diagnosis is an hypothesis concerning derived character states of the most recent common ancestor of a monophyletic group and differs in important respects from diagnoses in nonphylogenetic classifications (Rowe, 1987). Most significantly, apomorphic traits of an ancestor may be transformed in descendant taxa, so that a phylogenetically diagnostic character state is not necessarily shared by all members of the group in question.

TRIBE ORYZOMYINI VORONTSOV, 1959

PHYLOGENETIC DIAGNOSIS: Members of the Neotropical muroid complex (previously diagnosed in this report) descended from a common ancestor with the following traits: (1) a pectoral pair of mammae (mammary counts of eight or more in all known descendant taxa); (2) a long palate with prominent posterolateral pits (reversed in *Holochilus sciureus* which has a markedly shorter palate); (3) no alisphenoid strut separating the buccinator-masticatory and accessory oval foramina (reversed in *Holochilus* and some species of *Oligoryzomys*); (4) no posterior suspensory process of the squamosal attached to the tegmen tympani (secondary overlap between tegmen tympani and squamosal occurs in *Lundomys* and some species of *Oecomys*, but the contact never involves a distinct suspensory process of the latter bone); and (5) no gall bladder.

CONTENTS: *Holochilus*, *Lundomys*, †*Megalomys*, *Melanomys*, *Microryzomys*, *Neacomys*, *Nectomys*, *Nesoryzomys*, *Oecomys*, *Oligoryzomys*, *Oryzomys*, *Pseudoryzomys*, *Scolomys*, *Sigmodontomys*, *Zygodontomys*.

REMARKS: The phylogenetic classification of tylomyines and "thomasomyines," previously included in the Oryzomyini by Vorontsov (1959) and Reig (1980, 1984, 1986), is discussed by Carleton (1980) and Voss (1993), respectively. Except by including four tetralophodont genera, our tribal concept coincides with the narrow-sense oryzomyine group of Hershkovitz (1944, 1960). The implied reduction and loss of the mesoloph(id) in one or more clades descended from a pentalophodont oryzomyine ancestor were discussed by Voss (1991), and we note that either of the phylogenetic topologies illustrated

in figure 15 could provide the outline for an appropriate evolutionary scenario.

Some of the derived character states attributed to the oryzomyine ancestor in our phylogenetic diagnosis have not been surveyed in all hypothesized members of the tribe because only anatomically incomplete specimens are available for many species. We predict that future morphological research will require emendments to our phylogenetic diagnosis: additional homoplastic character transformations will doubtless be discovered, but more tribal synapomorphies may also be found, and new member genera remain to be described.

NATURAL HISTORY AND ZOOGEOGRAPHY

NATURAL HISTORY

Lundomys molitor is not a common rat in zoological collections, and ecological information is correspondingly scant. The first known Recent specimens, collected by C. C. Sanborn in 1926, were not recognized as distinct from sympatric *Holochilus brasiliensis* until Hershkovitz (1955) described them as *H. magnus*. Sanborn (1929) remarked that *H. "vulpinus"* (comprising his series of *H. brasiliensis* and *L. molitor*) "... was rather common along the Rio Cebollati and in some marshes in Trienta y Tres [Uruguay]. One was shot at night by shining its eyes with a jacklight."

Natural history data reported by Barlow (1969) were derived from 11 specimens of *Lundomys molitor* obtained by the American Museum of Natural History expedition to Uruguay in 1962–63. Seven of these were trapped by M. D. Tuttle (at two localities described below), and four were purchased from Sr. Marcellino Sanchez (who caught them in the Bañado de Tropa Vieja); the latter were subsequently prepared by Barlow and R. G. Van Gelder in Montevideo. Barlow (1969) abstracted habitat descriptions for *L. molitor* from Tuttle's fieldnotes, but omitted many details and did not acknowledge his source; rather than paraphrasing Tuttle again, we quote his field observations verbatim below.

The AMNH expedition camped from 7–

19 April 1963 near the Río Olimar Chico, about 25 km WSW Trienta y Tres, Departamento Trienta y Tres. The local vegetation (fig. 17) consisted of a low riparian woodland surrounded by rolling, grassy plains heavily grazed by cattle and sheep. Thermometer recordings (in S. Anderson's fieldnotes) documented an average 24-hour minimum temperature of 48°F and an average 24-hour maximum of 72°F at this camp. Tuttle's trapline was set along a small stream about one-half mile from the river:

At about 4:30 pm I began setting 50 rat traps along the stream near where I caught the [*Oligoryzomys delticola*] last night. I set the traps from 15 to 25 feet apart on both sides of the stream. I waded down the stream and set the traps along the banks. Most of the portion of the stream where my traps are set is well shaded by trees [and] there are many large ferns overhanging the stream. The stream banks are about 6 feet high, and the ferns and moss grow on these banks. Above, on the level, are ... sagebrush-like plants up to 5 feet tall and spaced about 8 feet apart. Beneath these bushes is ... grass about a foot tall. [Tuttle's notes for 10 April]

The following day, 11 April, this trapline caught nothing, but on the morning of 12 April the first of two specimens of *Lundomys molitor* taken at this locality (AMNH 206392) was found in a trap

... about 2 feet from the edge of the stream, which is about 4 feet wide at that point. The water was only 6 inches deep, but about 30 feet downstream there are several places where it is up to 2 feet deep. The trap was placed in an indistinct runway in grass about 9 inches tall. For about 250 feet up- and downstream the banks are about 6 feet high and covered with ferns whose fronds are up to 4 feet long and overhang the water. The trees, mostly less than 25 feet tall, are dense enough that very little direct sunlight reaches the stream. The [specimen] had 3 embryos, 1 in the right [uterine] horn and 2 in the left, each about 12 mm long, crown-rump. [Ibid., 12 April]

On 14 April another specimen (AMNH 206393), an adult male, was trapped

... about 400 feet from where the last was taken. It was caught in a trap placed beneath a large fern at the entrance to a runway coming from the stream, which was about 3 feet below the trap and over about a foot. The stream [here] is about 1.5 feet deep and 3.5 feet wide ... [and] about half-shaded by trees ... The upper portions of [the] stream bank are covered with a thin-bladed grass about 10 inches tall. Just above the water level, the banks are nearly entirely covered by liverworts and a little moss. There are runways about 2.5 inches in diameter [through] the grass, and



Fig. 17. The Río Olimar Chico, about 25 km WSW Trienta y Tres, in Departamento Trienta y Tres, Uruguay. M. D. Tuttle's two specimens of *Lundomys molitor* from this locality were trapped beside a small stream about one-half mile from the river. The landscape of open, rolling plains broken by gallery forests along shallow watercourses is characteristic of much of the country. Photographed by A. Ximénez in April 1963.

the liverworts have been worn away in a few areas just above water level. [Ibid., 14 April]

Tuttle tried to trap more *Lundomys molitor*, with additional rat traps, small Conibear traps, and small leghold traps, on the evening of 14 April. These were set where the stream was deeper (to 3 ft) and unshaded by trees; ferns, liverworts, and moss were almost completely absent from the streambank along this extended portion of the trapline. The traps were set within 10 in. of the water, and the Conibears were placed in the entrances to burrows that Tuttle thought might belong to *L. molitor*. Neither these nor other traps set for *L. molitor* along unshaded streamsides were successful here. The only other muroid species collected beside streams at this locality was *Oligoryzomys delticola*, but two specimens of *Reithrodon physodes* were trapped on adjacent hillsides.

From 21–25 May 1963, Tuttle worked on

the estancia of Sr. Julio Gerber, 3 km E Cardona in Departamento Soriano. On his first day there he set 49 rat traps along a stream

... only about 6 inches deep and 4 or 5 feet wide which forms ponds as much as 100 feet long and 50 feet wide ... In some areas there are water hyacinths in the stream, and cattails, rushes, and reeds, as well as a little *Eryngium* [Umbelliferae], grow at the stream's edge. Grass is about 3 feet tall for about 700 ft by about 150 ft along the stream [and] between it and a fence. ... There is a nearly continuous layer of fine, light green grass and clover beneath the taller grass. I placed the 49 rat traps along the stream's edge and ... 48 Museum Specials beneath the 3-foot grass on the higher but quite damp part of the area. [Tuttle's notes for 21 May]

On the following morning these traplines yielded a real bonanza.

In the 25 rat traps which I set beneath bunches of grass with blades about ... three feet tall right at the water's edge ... I caught 2 *Scapteromys [tumidus]* and 3 *Holochilus brasiliensis*. In the 24 rat traps set

... at the stream's edge on the other side of the fence where the grass with blades ... up to 4 feet tall, a little *Eryngium*, and many rushes, reeds, and cattails grow, I caught 13 *Scapteromys* [tumidus] and 1 [*Lundomys molitor*; AMNH 206368]. In the 48 Museum Specials set beneath grass about 3 feet tall in a wet area with a fine light green grass and clover growing beneath ... I caught 3 *Akodon* [azarae], 1 *Oxymycterus nasutus*, and 11 *Scapteromys* [tumidus]. [Ibid., 22 May]

Tuttle rebaited his traps on the afternoon of the 22nd, but caught only 3 *Scapteromys tumidus* (all in rat traps) on the 23rd. All the traps were rebaited again and 15 rat traps were moved to a new area along the stream. On the next morning, the streamside rat traps produced 11 *S. tumidus*, one *Holochilus brasiliensis*, and one *Lundomys molitor* (AMNH 206373). The latter

... was caught beneath a dense growth of rushes about 9 feet tall at the edge of a relatively open area. In general, I believe that [*Lundomys molitor*] is most often found in protected areas where there is more cover, and that [*Holochilus*] *brasiliensis* is most common in the open areas. [Ibid., 24 May]

This is the last entry in Tuttle's notes that provides ecological observations unambiguously associated with specimens of *Lundomys molitor*, but on the night of 25 May he shot 11 rats that were found swimming in the same stream; nine were *Holochilus brasiliensis*, and two were *L. molitor* (AMNH 206380, 206381), but Tuttle assumed that all were *H. brasiliensis* when he wrote up his notes that evening. The last specimen of *L. molitor* collected at this locality (AMNH 206388) was taken on the 27th, but no associated habitat information was recorded in Tuttle's journal or field catalog.

Tuttle's fieldnotes provide unambiguous evidence that *Lundomys molitor* is nocturnal, semiaquatic, and occurs sympatrically with *Holochilus brasiliensis* at some localities. The numbers of animals collected both by trapping and by night hunting from 22–27 May further suggest that *L. molitor* is less abundant than sympatric *H. brasiliensis*, but the available data are inadequate to infer possible ecological differences between these rats. The predominantly herbivorous habits of *Holochilus* are well documented (Martino and Aguilera, 1989; Twigg, 1962, 1965), but the diet of *Lundomys* is essentially unknown. Hershkovitz (1955) thought that *L. molitor*

might be the mollusc-eating rodent described by Burmeister (1879), but Barlow (1969: 41) found primarily "... macerated greenish plant material" in three stomachs (presumably from the specimens collected by Sr. Sanchez in the Bañado de Tropa Vieja). Our examination of the contents of two stomachs (AMNH 206373, 206388) from Tuttle's Soriano series of *L. molitor* revealed only crushed and chopped fibrous tissue; we did not attempt any histological analysis to determine whether this was of animal or vegetable origin, but we saw no identifiable animal parts in either stomach.

Tuttle's efforts to collect *Lundomys molitor* near the Río Olimar Chico by placing Conibear traps at burrow entrances were probably unsuccessful because *L. molitor* builds nests that are supported above the water in reeds (Sierra de Soriano, 1969: 483–484):

[*Lundomys molitor*] construye sus nidos sobre el agua, con profundidades que en nuestros registros alcanzan hasta 1,50 m; los mismos presentan forma esférica y se encuentran entre juncuales, de los que la rata extrae los materiales que utiliza en la construcción. Los nidos propiamente dichos están apoyados en los mismos juncos cortados a una altura de aproximadamente 80 cm sobre el nivel del agua, en un área modificada por el animal, que abarca alrededor de 60 cm²; los refugios están normalmente a unos 20 cm de la superficie del agua, con diámetros máximos y mínimos de 30 y 25 cm y altura de 9 a 11 cm; las paredes que lo forman presentan tres capas con diferentes grados de elaboración: la externa con un espesor de entre 4,5 y 5,0 cm está formada por trozos de juncos quebrados por incisión pero unidos por la corteza; dichos sectores aparecen entretejidos; en la capa media, los juncos están totalmente seccionados, tienen menor longitud (10–15 cm), y corresponden en general a los extremos apicales, apareciendo inflorescencias secas también quebradas por los incisivos de las ratas; en la pared interna, con un espesor de 4 a 5 cm, los trozos de juncos son cortos (de 2 a 5 cm) y se encuentran roídos y demenzados, formando una cobertura interna del nido, que aparece entonces totalmente tapizado incluso en el techo.

El refugio presenta además un vestíbulo con una rampa inclinada que conecta al nido con el agua y viceversa, formada también por trozos de juncos que se encuentran cortados totalmente y entretejidos, con longitudes de 25 a 30 cm aproximadamente.

It is noteworthy that *Holochilus brasiliensis* and *H. sciureus* also build elevated nests (Barlow, 1969; Twigg, 1962, 1965). Nests made by Guyanese *H. sciureus* in sugarcane fields (Twigg, 1965) correspond in several details of construction with those described above for *Lundomys molitor*.

ZOOGEOGRAPHY

Recent populations of *Lundomys molitor* are known to occur between about 29 and 35° S in Uruguay and Rio Grande do Sul (fig. 7) where grasslands, marshes, gallery forests, and open woodlands form a complex mosaic of subtropical pampas habitats (Barlow, 1969; Belton, 1984). The Lagoa Santa fossils (collected in the tropics near 19°38'S) therefore document a considerable northward extension of the species at some time in the Pleistocene or early Holocene. *Myocastor coypus*, another rodent currently restricted to subtropical and temperate latitudes (Redford and Eisenberg, 1992: map 11.112), is also represented by fossils from Lagoa Santa.⁷ As noted by Cerqueira (1982), such paleontological

range extensions suggest that prehistoric climates in Minas Gerais were at least periodically cooler than today's. Palynological data from a peat core collected at 19°S in Minas Gerais (Ledru, 1993) provide corroborating evidence of marked environmental changes over the last 30,000 years including cold-dry and cold-moist climatic episodes. Additional examples of species currently living elsewhere but locally extinct may be discovered among the fossils that Winge (1887) named *Habrothrix clavigensis*, *Habrothrix angustidens*, *Oxymycterus talpinus*, *O. cosmodus*, *Calomys anoblepas*, and *C. coronatus* (Voss and Myers, 1991). Much yet remains to be learned from Lund's paleontological legacy.

REFERENCES

- Aguilera, M., and A. Pérez-Zapata
1989. Cariología de *Holochilus venezuelae* (Rodentia, Cricetidae). Acta Cient. Venezolana 40: 198–207.
- Azara, F. de
1801. Essais sur l'histoire naturelle des quadrupèdes de la Province du Paraguay, vol. 2. Paris: Charles Pougens.
- Baker, R. J., B. F. Koop, and M. W. Haiduk
1983. Resolving systematic relationships with G-bands: A study of five genera of South American cricetine rodents. Syst. Zool. 32: 403–416.
- Barlow, J. C.
1969. Observations on the biology of rodents in Uruguay. Life Sci. Contr. R. Ontario Mus. 75: 59 pp.
- Belton, W.
1984. Birds of Rio Grande do Sul, Brazil. Part 1. Reheidae through Furnariidae. Bull. Am. Mus. Nat. Hist. 178: 369–636.
- Bond, M., and E. Massoia
1981. La presencia de *Holochilus magnus* (Rodentia, Cricetidae) en el Pleistoceno superior de la provincia de Buenos Aires. Circ. Inform. Assoc. Paleontol. Argentina 8: 11.
- Braun, J. K.
1993. Systematic relationships of the tribe Phyllotini (Muridae: Sigmodontinae) of South America. Oklahoma Mus. Nat. Hist. Spec. Publ.: 50 pp.
- Bugge, J.
1970. The contribution of the stapelial artery to the cephalic stapelial supply in muroid rodents. Acta Anat. 76: 313–336.
- Burmeister, H.
1879. Description physique de la République Argentine, tome III. Animaux vertébrés, pt. 1. Mammifères vivants et éteints. Buenos Aires: Paul-Emile Coni (Paris: F. Savy).
1961. Catálogo de los mamíferos de América del Sur. Rev. Mus. Argentina Cienc. Nat. "Bernardino Rivadavia" 4(2): 309–732.
- Carleton, M. D.
1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Misc. Publ. Mus. Zool. Univ. Michigan 146: 43 pp.
1980. Phylogenetic relationships in neotomine-peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Misc. Publ. Mus. Zool. Univ. Michigan 157: 146 pp.
1989. Systematics and Evolution. In G. L. Kirkland Jr. and J. N. Layne (eds.), Advances in the study of *Peromyscus* (Rodentia), pp. 7–141. Lubbock: Texas Tech Univ. Press.
- Carleton, M. D., and G. G. Musser
1984. Muroid rodents. In S. Anderson and J.

⁷ Reported as *Myopotamus castoroides* by Winge (1887) from the caves that Lund called Lapa do Bahu, Lapa da Cerca Grande, Lapa da Escrivania Nr. 1 and Nr. 11, Lapa da Serra das Abelhas, Lapa da Serra da Anta, and Lapa dos Tatus. It should be noted that although remains of *Myocastor coypus* and *Lundomys molitor* were both excavated from Lapa da Escrivania, they occurred in separate chambers of the cave.

- K. Jones (eds.), Orders and families of Recent mammals of the world, pp. 289–379. New York: Wiley.
1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microroryzomys*. Bull. Am. Mus. Nat. Hist. 191: 83 pp.
- Cerqueira, R.
1982. South American landscapes and their mammals. In M. A. Mares and H. H. Genoways (eds.), Mammalian biology in South America. Pymatuning Lab. Ecol., Spec. Publ. Ser. 6: 53–75.
- Ellerman, J. R.
1941. The families and genera of living rodents, vol. 2. Muridae. London: British Museum (Natural History).
- Freitas, T. R. O., M. S. Mattevi, L. F. B. Oliveira, et al.
1983. Chromosome relationships in three representatives of the genus *Holochilus* (Rodentia, Cricetidae) from Brazil. Genetica 61: 13–20.
- Gyldenstolpe, N. C. G.
1932. A manual of Neotropical sigmodont rodents. Kungl. Svenska Vetenskapsakad. Handl. Ser. 3, 11(3): 164 pp. + 18 pls.
- Hatting, T.
1980. Den danske Zoolog P. W. Lund og hans udforskning af Brasiliens knoglehuler. Copenhagen: Zoologisk Museum.
- Hershkovitz, P.
1944. A systematic review of the Neotropical water rats of the genus *Nectomys* (Cricetinae). Misc. Publ. Mus. Zool. Univ. Michigan 58: 101 pp. + folding map.
1955. South American marsh rats, genus *Holochilus*, with a summary of sigmodont rodents. Fieldiana: Zoology 37: 639–673 + pls. 17–29.
1960. Mammals of northern Colombia, preliminary report No. 8: Arboreal rice rats, a systematic revision of the subgenus *Oecomys*, genus *Oryzomys*. Proc. U.S. Nat. Mus. 110: 513–568.
1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana: Zoology 46: 524 pp.
1966. South American swamp and fossorial rats of the scateromyine group (Cricetinae, Muridae) with comments on the glans penis in muroid taxonomy. Z. Säugetierkd. 31: 81–149.
1967. Dynamics of rodent molar evolution: a study based on New World Cricetinae, family Muridae. J. Dent. Res. 46(5, suppl.): 829–842.
- Hinton, M. A. C.
1926. Monograph of the voles and lemmings (Microtinae) living and extinct, vol. 1. London: British Museum (Natural History).
- Hooper, E. T.
1962. The glans penis in *Sigmodon*, *Sigmodon*, and *Reithrodon* (Rodentia, Cricetinae). Occas. Pap. Mus. Zool. Univ. Michigan 625: 11 pp.
- Hooper, E. T., and G. G. Musser
1964. The glans penis in Neotropical cricetines (Muridae) with comments on classification of muroid rodents. Misc. Publ. Mus. Zool. Univ. Michigan 123: 57 pp.
- Janis, C. M., and M. Fortelius
1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biol. Rev. Cambridge Philos. Soc. 63: 197–230.
- Kluge, A. G., and J. S. Farris
1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18: 1–32.
- Ledru, M.-P.
1993. Late Quaternary environmental and climatic changes in central Brazil. Quaternary Res. 39: 90–98.
- Lezcano, M. J., C. Reboledo, and C. E. Schreiber
1992. Bioestratigrafía de los sedimentos de la cuenca alta del río de La Reconquista (Pleistoceno tardío, noreste del la provincia de Buenos Aires, Argentina). Ameghiniana 29: 387.
- Maddison, W. P., and D. R. Maddison
1992. MacClade, version 3: Analysis of phylogeny and character evolution [computer program and user's manual]. Sunderland, MA: Sinauer.
- Martino, A. M. G., and M. Aguilera M.
1989. Food habits of *Holochilus venezuelae* in rice fields. Mammalia 53: 545–561.
- Massoia, E.
1974. Ataques graves de *Holochilus* y otros roedores a cultivos de caña de azúcar. Inst. Nac. Tec. Agrop., Idia 321/24: 1–12.
1980. El estado sistemático de cuatro especies de cricétidos sudamericanos y comentarios sobre otras especies congénicas (Mammalia–Rodentia). Ameghiniana 17: 280–287.
1981. El estado sistemático y zoogeografía de *Mus brasiliensis* Desmarest y *Holochilus sciureus* Wagner (Mammalia, Rodentia, Cricetidae). Physis, Secc. C, 39(97): 31–34.

- Moojen, J.
1952. Os roedores do Brasil. Rio de Janeiro: Instituto Nacional do Livro.
- Musser, G. G., and M. D. Carleton
1993. Family Muridae. In D. E. Wilson and D. M. Reeder (eds.), *Mammal species of the World: A taxonomic and geographic reference*, 2nd ed., pp. 501–755. Washington, D.C.: Smithsonian Institution Press.
- Olds, N., and S. Anderson
1989. A diagnosis of the tribe Phyllotini (Rodentia, Muridae). In K. H. Redford and J. F. Eisenberg (eds.), *Advances in Neotropical mammalogy*, pp. 55–74. Gainesville: Sandhill Crane Press.
- Paula Couto, C. de
1950. Lund e suas obras no Brasil. In P. W. Lund, *Memórias sobre a paleontologia brasileira* [translated works of Lund edited by C. de Paulo Couto], pp. 27–66. Rio de Janeiro: Instituto Nacional do Livro.
- Pearson, O. P., and J. L. Patton
1976. Relationships among South American phyllotine rodents based on chromosome analysis. *J. Mammal.* 57: 339–350.
- Redford, K. H., and J. F. Eisenberg
1992. *Mammals of the Neotropics*, vol. 2: The Southern Cone. Chicago: Univ. Chicago Press.
- Reig, O.
1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). *J. Zool. London* 181: 227–241.
1980. A new fossil genus of South American cricetid rodent allied to *Weidomys*, with an assessment of the Sigmodontinae. *J. Zool. London* 192: 257–281.
1984. Distribuição geográfica e história evolutiva dos roedores muroides sulamericanos (Cricetidae: Sigmodontinae). *Rev. Brasil. Genet.* 7: 333–365.
1986. Diversity patterns and differentiation in high Andean rodents. In F. Vuilleumier and M. Monasterio (eds.), *High altitude tropical biogeography*, pp. 404–439. New York: Oxford Univ. Press.
- Rensberger, J. M.
1973. An occlusion model for mastication and dental wear in herbivorous mammals. *J. Paleontol.* 47: 515–528.
- Rowe, T.
1987. Definition and diagnosis in the phylogenetic system. *Syst. Zool.* 36: 208–211.
- Sanborn, C. C.
1929. The land mammals of Uruguay. *Field Mus. Nat. Hist. (Zool. Ser.)* 17: 147–165.
- Sierra de Soriano, B.
1965. Algunas estructuras externas relacionadas con la vida anfibia en dos especies del género *Holochilus* Brandt, 1835 (Muridae, Cricetinae). *Rev. Fac. Hum. Cienc.* 22: 209–220.
1969. Algunos caracteres externos de cricétinos y su relación con el grado de adaptación a la vida acuática (Rodentia). *Physis* 28: 471–486.
- Simpson, G. G.
1984. Discoverers of the lost world. An account of those who brought back to life South American mammals long buried in the abyss of time. New Haven: Yale Univ. Press.
- Smithe, F. B.
1975–1981. *Naturalist's color guide*. New York: Am. Mus. Nat. Hist.
- Stehlin, H. G., and S. Schaub
1951. Die Trigonodontie der simplicidentaten Nager. *Schweitzer. Paleontol. Abh.* 67: 385 pp.
- Swofford, D. L.
1993. PAUP: Phylogenetic analysis using parsimony, Version 3.1 (computer program distributed by the Illinois Natural History Survey, Champaign, IL).
- Swofford, D. L., and D. P. Begle
1993. User's manual, PAUP Version 3.1 (distributed with computer program by the Illinois Biological Survey, Champaign, IL).
- Tate, G. H. H.
1932. [Taxonomic histories of South and Central American cricetid rodent genera]. *Am. Mus. Novitates* 529, 541, 562, 579, 580, 581, 582, and 583.
- Thomas, O.
1917. On the arrangement of the South American rats allied to *Oryzomys* and *Rhipidomys*. *Ann. Mag. Nat. Hist.* 8(20): 192–198.
1928. The Godman-Thomas expedition to Peru.—VII. The mammals of the Rio Ucayali. *Ann. Mag. Nat. Hist.* 10(2): 247–265.
- Trouessart, E.-L.
1898. *Catalogus mammalium tam viventium quam fossilium*, nova editio, tomus 1. Berlin: R. Freiländer & Sohn.
- Twigg, G. I.
1962. Notes on *Holochilus sciureus* in British Guiana. *J. Mammal.* 43: 369–374.
1965. Studies on *Holochilus sciureus berbicensis*, a cricetine rodent from the coastal

- region of British Guiana. *Proc. Zool. Soc. London* 145: 263–283.
- Vidal, O. R., R. Riva, and N. I. Baro
1976. Los cromosomas del género *Holochilus* I. Polimorfismo en *H. chacarius* Thomas (1906). *Physis, Secc. B*, 35(90): 75–85.
- Vorontsov, N. N.
1959. The system of hamster (Cricetinae) in the sphere of the world fauna and their phylogenetic relations [in Russian]. *Biul. Mosk. Obsh. Isp. Prir. Otd. Biol.* 64: 134–137.
1979. Evolution of the alimentary system in myomorph rodents. New Delhi: Indian National Science Documentation Centre [published for the Smithsonian Institution].
- Voss, R. S.
1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bull. Am. Mus. Nat. Hist.* 188: 259–493.
1991. An introduction to the Neotropical muroid rodent genus *Zygodontomys*. *Bull. Am. Mus. Nat. Hist.* 210: 113 pp.
1992. A revision of the South American species of *Sigmodon* (Mammalia: Muridae) with notes on their natural history and biogeography. *Am. Mus. Novitates* 3050: 56 pp.
1993. A revision of the Brazilian muroid rodent genus *Delomys* with remarks on “thomatomyine” characters. *Am. Mus. Novitates* 3073: 44 pp.
- Voss, R. S., and P. Myers
1991. *Pseudoryzomys simplex* (Rodentia: Muridae) and the significance of Lund’s collections from the caves of Lagoa Santa, Brazil. *Bull. Am. Mus. Nat. Hist.* 206: 414–432.
- Wagner, A.
1842. Beschreibung einiger neuer oder minder bekannter Nager. *Archiv Naturg.* 8(1): 1–33.
- Winge, H.
1887. Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. *E Museo Lundii* 1(3): 200 pp. + 8 pls.
1941. The interrelationships of the mammalian genera, vol. 2. Copenhagen: C. A. Reitzels Forlag.

APPENDIX

Reanalysis of Data from G-banded Chromosomes

Baker et al. (1983) reported data from G-banded chromosomes of 16 New World muroids and attempted to infer phylogenetic relationships from patterns of shared and apparently derived rearrangements. The species represented in their study (table 6) included one neotomine (*Neotoma micropus*) together with *Sigmodon hispidus*, *Holochilus “brasiliensis”* (= *H. sciureus* in the sense of this report), and 13 oryzomyines (sensu Hershkovitz, 1944, 1960). Baker et al. (1983) found sufficient resolution in G-band patterns to suggest homologies for the 12 largest autosomal pairs in each karyotype and recorded banding similarities and differences among putative homologs. Banding patterns observed in *Neotoma micropus* and in one or more Neotropical taxa were presumed to be primitive, a procedure consistent with our own assumptions of ingroup monophyly and outgroup comparison. Unfortunately, Baker and his colleagues also assumed the monophyly of *Oryzomys* (sensu lato, including *Melanomys*, *Oecomys*, and *Oligoryzomys*) and used *Sigmodon*, *Nea-*

comys, *Nectomys*, and *Holochilus* as outgroups to infer polarities and order character states within the genus.

We doubt that *Oryzomys*, whether construed sensu lato (as by Baker et al., 1983) or in the more restricted sense of Musser and Carleton (1993), is monophyletic. The genus (in all past or current usages) is unrevised and no diagnostic synapomorphies are known. Membership in *Oryzomys* is therefore not an appropriate criterion for polarity estimation or character-state ordering, and phylogenetic analyses should not be constrained by assumptions of generic monophyly.

Because we could not evaluate the empirical basis for Baker et al.’s (1983) hypotheses of character-state ordering, we entered their data as unordered characters in an unweighted Wagner parsimony analysis implemented by the branch-and-bound algorithm of PAUP Version 3.1 (Swofford, 1993). Our matrix (table 6) is condensed from their table 1 by excluding uninformative or uninterpretable chromosomes (i.e., 7, 9, 10, 13, 14, and “A”). Tree topologies were rooted by designating *Neotoma micropus* as the outgroup. We updated the generic taxonomy to reflect current usage but made no attempt to verify the accuracy of

specific identifications (except as noted above for *Holochilus* “*brasiliensis*”).

A very large number of alternative phylogenetic topologies provide maximally parsimonious interpretations of these data. The strict consensus of 10,000 such equally shortest trees (each requiring 46 steps; fig. 16), however, supports Baker et al.’s (1983) conclusion that *Holochilus* is more closely related to oryzomyines than to *Sigmodon*. By comparison, trees in which *Sigmodon* and *Holochilus* are constrained to be sister taxa require at least three additional character state changes (49 total) to fit the karyotypic evidence.

TABLE 6
Character Data from G-banded Chromosomes
(See text for explanation)

Species ^a	Chromosomes ^b											
	C1	C2	C3	C4	C5	C6	C8	C-11	C-12			
<i>Neotoma micropus</i>	0	0	0	0	0	0	0	0	0			
<i>Sigmodon hispidus</i>	2	10	?	0	0	0	0	?	4			
<i>Neacomys guianae</i>	1	2	1	1	0	1	0	1	0			
<i>Nectomys squamipes</i>	0	1	2	1	0	2	0	5	1			
<i>Holochilus</i> “ <i>brasiliensis</i> ”	1	2	0	1	0	1	1	1	2			
<i>Oryzomys capito</i>	1	2	0	2	1	3	1	3	0			
<i>Oryzomys</i> sp.	1	3	0	2	1	3	1	3	0			
<i>Oryzomys palustris</i>	1	4	3	1	0	1	?	1	3			
<i>Melanomys caliginosus</i>	1	5	3	1	0	1	?	1	3			
<i>Oryzomys couesi</i>	1	4	3	1	0	1	?	1	3			
<i>Oryzomys caudatus</i>	1	6	4	2	0	1	?	3	0			
<i>Oecomys concolor</i>	3	3	0	?	?	?	?	3	0			
<i>Oligoryzomys delicatus</i>	1	7	7	3	2	?	1	4	?			
<i>Oecomys bicolor</i>	4	8	5	4	3	?	1	2	0			
<i>Oryzomys melanotis</i>	1	3	0	2	0	1	1	3	0			
<i>Oryzomys alfaroi</i>	1	9	6	5	4	4	1	6	?			

^a Generic taxonomy updated to reflect current usage, but sequence of taxa and species names follow Baker et al. (1983: table 1).

^b Chromosomal character states in Baker et al. (1983: table 1) recoded for PAUP analysis as follows: ? = unidentified segments; 0 = identical to *Neotoma micropus*; 1 = Mⁱ (an alternative modification, arbitrarily numbered); 2 = Mⁱⁱ; 3 = Mⁱⁱⁱ; etc.

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